TEMPORAL PATTERNS OF LOCOMOTOR ACTIVITY IN HATCHLING SEA TURTLES

By

SHERI A. DALTON

A DISSERTATION PRESENTED TO THE GRADUATE COUNCIL OF
THE UNIVERSITY OF FLORIDA
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE
DEGREE OF DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

1979

To the Graduate Student Union.

ACKNOWLEDGMENTS

The assistance and cooperation of many people at the University of Florida were invaluable in the course of this study. I am especially grateful, for their aid and patience, to the members of my committee: Dr. J. H. Kaufmann, Dr. A. F. Carr, and Dr. H. O. Schwassmann of the Department of Zoology, and Dr. M. C. Yang of the Department of Statistics. I also thank my fellow graduate students and undergraduate assistants for their advice and support.

I would like to thank Dr. N. Mrosovsky of the University of Toronto, Dr. C. R. Shoop of the University of Rhode Island and Dr. D. W. Ehrenfeld of Rutgers University for their excellent advice on the care and feeding of young sea turtles, and I am especially indebted to Dr. Ralph Ackerman and to Dr. J. Perran Ross for the care they showed in collecting the turtles used in this investigation.

The facilities of the Department of Natural Sciences of the Florida State Museum were kindly made available by Dr. W. Auffenberg for the purpose of this study, and in this regard I must thank the Natural Sciences faculty, staff and students for their thoughtfulness during the times experiments were in progress.

The Northwest Regional Data Center, Gainesville, provided the computer facilities used in the analysis of data collected during the course of this project.

I must express my gratitude to Dr. J. F. Bartholic of Fruit Crops, I.F.A.S., for allowing me the use of several pieces of laboratory

equipment, and I am also grateful to Mr. Frank Davis, Electrical Technician, for his advice regarding the construction of my recording tanks.

I would especially like to thank Ms. Donna Gillis for her skillful typing of the manuscript and for extensive support during its preparation.

Finally, I express my gratitude to Dr. B. S. Beals, supervisor of my M.A. research, for her encouragement to continue in graduate school.

TABLE OF CONTENTS

	Page
ACKNOWLEDGMENTS	iii
ABSTRACT	vi
INTRODUCTION	1
MATERIALS AND METHODS	4
The Turtles	4
Recording Apparatus	9
Preliminary Data Analysis	14
THE SWIMMING FRENZY	18
Procedure	19
Results	25
Discussion	43
TEMPORAL PATTERNS OF LOCOMOTOR ACTIVITY	52
Temporal Distribution of Activity Under Natural Light-Dark Cycles	56
The Free-Running Period and the Effect of Photofraction	78
Tidal Rhythms	113
Summary of Results	118
Discussion	122
PATTERN DEVELOPMENT	128
Procedure	128
Results and Discussion	129
APPENDIX	
I THE ANALYSIS OF BIOLOGICAL TIME SERIES	141
II SYMBOLS AND ABBREVIATIONS	146
LITERATURE CITED	149
BIOGRAPHICAL SKETCH	155

Abstract of Dissertation Presented to the Graduate Council
of the University of Florida in Partial Fulfillment of the Requirements
for the Degree of Doctor of Philosophy

TEMPORAL PATTERNS OF LOCOMOTOR ACTIVITY IN HATCHLING SEA TURTLES

By

Sheri A. Dalton

June, 1979

Chairman: John H. Kaufmann
Major Department: Zoology

Little is known regarding the whereabouts and activities of sea turtles under the age of one year. The present laboratory study was an attempt to obtain information on the temporal distribution of swimming activity in hatchling *Chelonia mydas mydas* and *Chelonia mydas agassizi* during the swimming frenzy and during subsequent months. Turtles were exposed to various light-dark cycles and to constant light and temperature.

The swimming frenzy of green turtle hatchlings from Ascension Island was distinctly different from that of green turtles from Tortuguero, Costa Rica. Only half of the Ascension Island turtles showed any frenzy. They swam for an average of 8.28 ± 3.29 hours during a two-day frenzy. The Tortuguero hatchlings were of two apparently genetic size classes, large and small, and each class had a distinctive frenzy. Ninety per cent of the small hatchlings showed a three-day frenzy involving 9.43 ± 4.22 hours of frenzied swimming, while the two-day frenzy of the large hatchlings involved only 3.03 ± 0.08 hours of strong swimming.

The distinct swimming frenzy activities of the two hatchling groups from Tortuguero may be based in genetic differences arising from the segregation of the parent turtles into two feeding and breeding populations, one from waters off Nicaragua and one from south of Tortuguero. The frenzy may serve to conduct the young into different current systems for their pelagic first year of life. Basic differences between the groups of green turtles studied were corroborated by the swimming frenzy experiments conducted under constant light.

The Pacific black turtles from the Galapagos Islands had all been exposed to water prior to their use in the study. Most showed no frenzy.

Examination of the temporal distribution of activity provided information on the photoperiodic entrainment characteristics of young green turtles. All turtles exhibited diurnal bimodally distributed swimming activity under "natural" photoperiods. This was transformed to a unimodal distribution if twilight was absent from the photophase to which Tortuguero hatchlings were exposed. The turtles may be crepuscular in their natural environment because of thermal inhibition of activity during the daylight hours.

Hatchling green turtles conformed to the general standard set by studies of homeotherms, in that their activity onset was more precisely timed than their activity offset. Seventy per cent of the hatchlings tested exhibited free-running periods of less than 24 hours, while 30% showed no measurable free-running period. The turtles maintained relatively stable distributions of activity over increasing photofractions. All turtles exhibited weak tidal rhythms.

The swimming activity rhythm of green turtle hatchlings may be based in a system of mutually synchronized oscillators, one coupled to dawn and one to dusk. Swimming activity may also be composed of separate but synchronized oscillators controlling various components of activity, such as the search for food, position adjustment and exploratory behavior, which may free-run with slightly different periodicities. This may have been the cause of the lack of precision demonstrated by the turtles in the timing of their periods.

The free-running periods demonstrated were not precise enough to be used as the basis for time-compensated sun-compass orientation. It is possible, though, that greater precision could be attained by turtles exposed to different light intensities or spectral compositions.

INTRODUCTION

Sea turtles have traveled the tropical oceans of this planet since the late Cretaceous (Carr and Coleman 1974) and have long been objects of worship and a major source of dietary protein for native peoples having access to their nesting and feeding grounds. In spite of this long association with man, however, they remain animals of mystery.

The five genera of sea turtles are characteristically inhabitants of the open ocean, found on shore at only two stages of their lives. The young hatch in deep nests above the tide line approximately two months after a female has come ashore to lay her eggs. After several days of communal upward scrabbling, the hatchlings emerge to scurry across the beach to the surf and thence to disappear for the first year of their lives (the "lost year").

The female, and possibly the male, returns every two or three years (see review by Carr *et al.* 1978) to a specific stretch of beach on which she herself may have been hatched. The nesting beaches of most species of sea turtles are several hundred kilometers from their feeding grounds and sea turtles are outstanding examples of a long distance migrator, apparently capable of precise orientation toward a learned or instinctive goal.

The migratory, marine lifestyle of these turtles renders them difficult subjects of study, and information concerning them has been gathered slowly. Research on the animals has been largely restricted

to investigations on the egg, the very young hatchling, the nesting female, and mature turtles held in zoos and turtle culture facilities. Interest in sea turtle research is widespread, however, and the gaps in our knowledge of them are steadily being filled.

The green turtle, *Chelonia mydas mydas*, is perhaps the best studied of all the sea turtles and has been the major subject of an ongoing research program directed by Dr. Archie Carr of the University of Florida. Its nesting populations at Ascension Island and Tortuguero, Costa Rica, have been under investigation for many years.

Tagging has shown that the Ascension Island nesting population (Carr 1975) consists of greens from feeding grounds to the north and south of the bulge of Brazil. The Tortuguero turtles are also separated into two groups: those using feeding grounds off Nicaragua and those using grounds to the south of Tortuguero nesting beaches. The two Costa Rican feeding populations may represent distinct genetic populations, which in turn may correspond to the two hatchling size classes (small and large) described by Ackerman (1975).

Hatchling turtles leaving these two nesting areas face significantly different environments. Ascension Island emerges abruptly from deep water and is bathed by the stable South Equatorial Current heading toward Brazil. The beach at Tortuguero, on the other hand, is bordered by a wide continental shelf and is washed by an unstable current system which is variable in strength as well as in direction of flow.

Neonate sea turtles are probably pelagic during their first year, and perhaps control the direction of their passive drift by positioning themselves in specific current systems. It is thought that such

positioning is one of the functions of the juvenile swimming frenzy, the seemingly frantic swimming exhibited by young turtles during their first few days in the water.

It is almost impossible to track hatchlings over long distances in the open ocean. Knowledge of the nature and duration of the frenzy in hatchlings kept in a controlled laboratory environment could allow an estimation of the position in the ocean gained by the young turtles at the end of their swimming frenzy. A description of the swimming frenzy was the object of the first portion of this investigation.

The features of sea turtle endogenous rhythms, like those of most other reptiles, are largely undescribed. It is assumed, however, that these poikilotherms share the free-running period and entrainment characteristics described for homeotherms. Examination of the swimming activity rhythms of hatchling sea turtles could help verify or refute this assumption, and so was made the goal of the second part of this investigation. Identification of a time-sense in the turtles could also indicate that they are capable of precise navigation during migration.

MATERIALS AND METHODS

The Turtles

Most of the turtles used in this study were *Chelonia mydas mydas* of unknown sex. They hatched from eggs collected during the 1972 to 1974 nesting seasons from the northern five miles of beach at Tortuguero, Costa Rica, or from the west coast of Ascension Island. Tortuguero young of both small and large hatching size classes (Ackerman 1975) were studied, since it is considered possible that they may represent the young of different genetic populations with feeding grounds to the north and south of Tortuguero. A few Pacific black turtle hatchlings, *Chelonia mydas agassizi*, were obtained in 1973. Egg collection was under the control of Dr. Archie Carr's assistants and graduate students, most notably Ralph Ackerman.

The eggs were transported by air to Gainesville where they were packed in moist sand in styrofoam containers for placement in incubators. They were then used in Ackerman's (1975) research into egg physiology and gas exchange. One result of his work worth noting is that the growth rates of his laboratory-reared embryos were similar to those recorded in natural nests. There is nothing to suggest that the later activity of these turtles should differ significantly from those undergoing a natural incubation and emergence.

At the first sign of hatching the turtles and their shells were removed from the incubator and placed in a single layer on moist paper

toweling in a light-tight styrofoam box. The hatchlings were left in the dark for the 24 to 48 hours necessary for full emergence from the shell plus an extra five days. This time was equivalent to that required for a natural mass emergence from the nest onto the beach surface (Raj 1976, Zwinenberg 1976) and allowed the laboratory-reared hatchlings to mature the appropriate length of time before their initial entry into the water. The five turtles to be used immediately in swimming frenzy experiments were then placed in another damp styrofoam container for transport to the experimental tanks. The rest were placed together in salt water aquaria.

At the time of emergence from the artificial nest, all hatchlings still had vestiges of a yolk sac and a large umbilical scar. Attempts at feeding were usually unsuccessful for the next three days, after which most of the hatchlings ate well. They were offered various combinations of finely chopped de-boned marine fish, squid, chicken hearts, chicken livers, and shrimp mixed with a crushed multiple vitamin tablet (one per five turtles) and a small amount of red food coloring. The turtles seemed to be able to locate the food with greater ease when it was dyed. It is unknown what green turtle hatchlings normally eat, but they are probably carnivorous (Carr 1965) and the diet provided was apparently adequate.

The hatchlings were fed in small pans containing a few centimeters of fresh water at room temperature. This prevented excessive fouling of the holding tanks. They were allowed to feed *ad lib* for at least one and one-half hours daily and longer if at all possible. The time spent in fresh water did them no evident harm (Kooistra and Evans 1976). The

reserve turtles were fed in groups because of space limitations, but the experimental animals were fed individually. All feeding took place during the photophase at randomly selected times in order to prevent any possible entrainment of activity rhythms by strictly periodic feedings.

The reserve turtles were maintained under LD conditions ranging from 11:13 to 14:10 depending upon the season. Light was provided by overhead fluorescent bulbs and large north-facing windows which gave an average daytime illumination level of 700 lux. The water was maintained at approximately 22°C. The major health problem encountered resulted from the tendency of turtles to nip at the flippers and eyes of others, causing open sores and necrosis in adjacent tissue. These wounds were treated with a wash of potassium permanganate or gentian violet to control the spread of infection. This was not a problem in the experimental animals which were individually housed and fed.

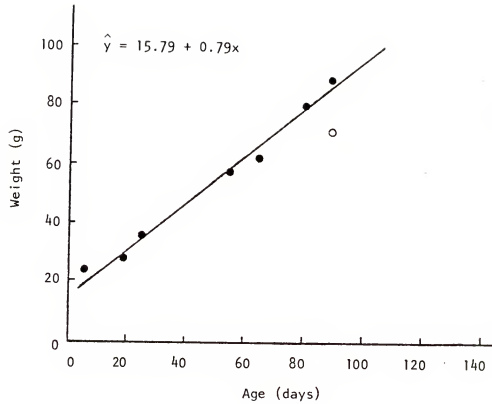
Carapace length to the nearest mm, convexity of plastron and weight to the nearest g were noted daily for all experimental turtles. A concave plastron indicated a turtle which was not feeding properly, and such a turtle was immediately replaced by a healthy reserve animal. Regressions of weight on age in days since full emergence from the egg and of weight on carapace length (Fig. 1) showed steady growth rates of approximately 0.79 g per day which were comparable to those reported by Kaufmann (1972). The weight and age data also show, as expected, that the individually housed and fed experimental hatchlings grew faster than those held in the reserve tanks.

Figure 1. Growth rates of hatchling green turtles of the small size class from Tortuguero, Costa Rica.

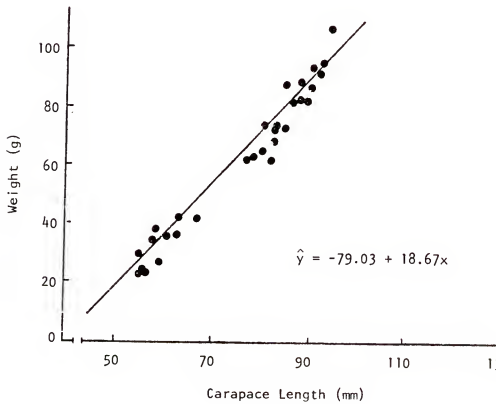
A. Weight as a function of age in green turtle hatchlings. Each closed circle represents the mean weight of a representative group of five turtles raised in separate tanks in the experimental room (LD+t12:12). The open circles represent mean weights of five turtles raised together in the holding tank to the age of 85 days and then transferred to the experimental tanks. The latter data were not used in calculation of the regression line.

B. Weight as a function of carapace length in ten green turtle hatchlings.

A


$\hat{y}$ = 15.79 + 0.79x
Weight (g)
Age (days)
0
20
40
60
80
100
120
140

B


$\hat{y}$ = -79.03 + 18.67x
Weight (g)
Carapace Length (mm)
50
70
90
110
130

Recording Apparatus

Experimental animals were housed individually in heavy-duty polyethylene tanks (Fig. 2) containing 25 cm of sea water from which all visible particulate matter had been removed. The pH of the water was monitored daily and remained within the acceptable range (Ehrenfeld personal communication) of 7.8 to 8.4. Specific gravity fluctuated between 1.020 and 1.025, well within the sea water range given in the CRC Handbook (Weast 1972). The tanks were cleaned each week and refilled with sea water from Marineland, Florida. The turtles were always fed outside the recording tanks, in order to reduce fouling of the water. Water temperature was controlled indirectly by a room air temperature thermostat set at 26°C. This temperature corresponded closely to the water temperatures within which green turtle hatchlings might be found under natural conditions (Anon, 1967). Air temperature and humidity were monitored continuously throughout all experiments (Figs. 3, 4).

The five experimental tanks were located in an underground light-tight room. Tank water passed constantly through Biozonics Salt Water Filters whose intakes and outlets were separated from the swimming channel by a perforated styrofoam panel. This eliminated "false" activation of the event recorder by filter-created currents. The constant background noise of the filters reduced the possibility of the turtles changing their activity levels in response to event recorder clicks and building noises. The 30-cm-wide swimming channel was constructed of 1.2 cm fiberglass-coated wire mesh and was large enough, with an outer diameter of 45 cm, to allow free movement of most turtles younger than six months.

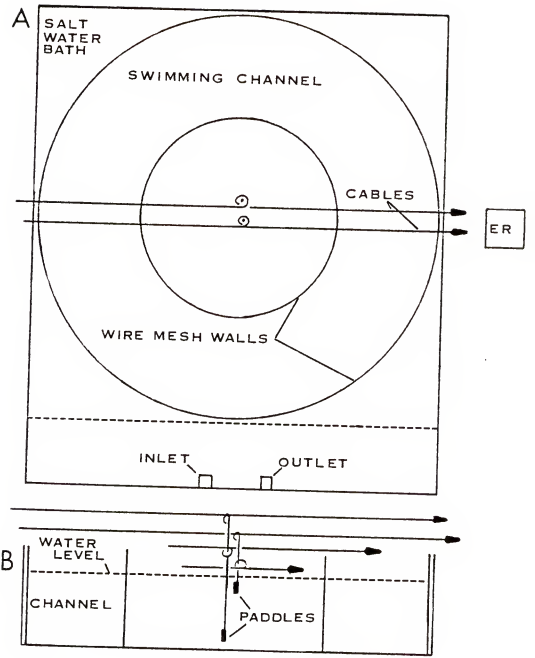


Figure 2. Schematic of the recording tank showing the relationship of the swimming channel to the foil paddles used as transducers of turtle swimming activity to the event recorder. A. Top view; B. Side view at level of large arrow.

ER Event recorder.

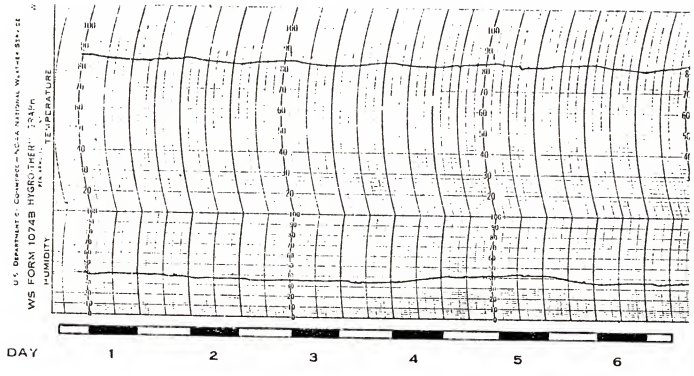


Figure 3. Hygrothermograph record for five days in the experimental room. Temperature was recorded in °F. LD12:12(270:01).

LIGHT
DARK

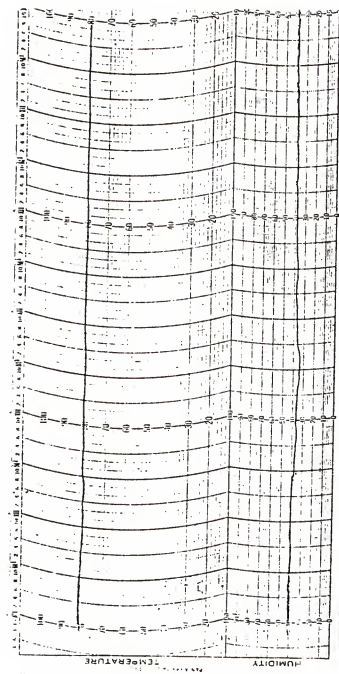


Figure 4. Hygrothermograph record for five days in the experimental room. LL(270).

The principal light sources in the experimental room were overhead standard fluorescent bulbs. Although Ehrenfeld (personal communication) suggested that the spectral output of these lamps might be inadequate for the maintenance of healthy turtles because the bulbs have a deficit in the red end of the spectrum (Elenbaas 1971), the turtles apparently remained healthy.

Light intensity was set by two rheostats, one controlling a bank of lights over the tanks, the other the lights over the remainder of the room. Each rheostat was controlled by a timing mechanism. The maximum ambient illumination which could be attained at the recording tanks was 270 lux. This is low in comparison with normal daylight illumination of 2.7×10^4 lux, but well within the photophase illumination levels commonly used in circadian rhythm studies on diurnal animals (Bünning 1973, Hoffmann 1968). Twilight, a step reduction or increase in light intensity, was imposed by setting the lights over the tanks to turn on later (dawn) or off earlier (dusk) than the lights over the rest of the room. The minimum twilight illumination which could be achieved at the tanks was 100 lux. Incandescent bulbs in reptile cages across the room were left on permanently, giving a scotophase light intensity over the tanks of 0.1 lux.

Water currents created by turtle flippers deflected two foil paddles suspended at depths of 1 and 21 cm in the core of the swimming channel. Sufficient movement of a paddle (2 mm in any horizontal direction) closed an electric circuit, creating a record of the activity on one channel of a 20 channel Esterline-Angus event recorder whose chart paper ran continuously at a speed of 15 cm per hour. This speed

was necessary to permit statistical analysis of the data (see Appendix 1), but prevented presenting the actogram in the standard fashion of vertically aligning the daily activity records. Artificial displacement of the water in the swimming channel, and observations of turtles in the tanks, verified that only the upper paddle recorded surface swimming. The lower paddle responded to activity near the bottom of the tank, and both paddles recorded activity in the middle. Activity in all areas of the swimming channels could be sensed by the recording apparatus.

The activity records gave no indication of the compass direction in which turtles were swimming. Absolute amounts of activity could only be estimated because the sensitivity of the apparatus varied slightly among the tanks. The records gave an accurate account only of activity patterns.

Examination of the record and simultaneous observation of the turtles provided a picture of the behavioral correlates of the activity records. Without such observation the information that can be drawn from a study of circadian rhythms and entrainment is severely limited (Enright 1970, Menaker 1976), as the activity record represents a summation of the physiological and behavioral states of the subject as well as its responses to exogenous environmental factors. Figure 5 illustrates the form of record obtained as a result of specific hatchling activities.

Preliminary Data Analysis

Jenkins and Watts (1968) define two major types of time series: continuous (as obtained from continuous measurements) and discrete

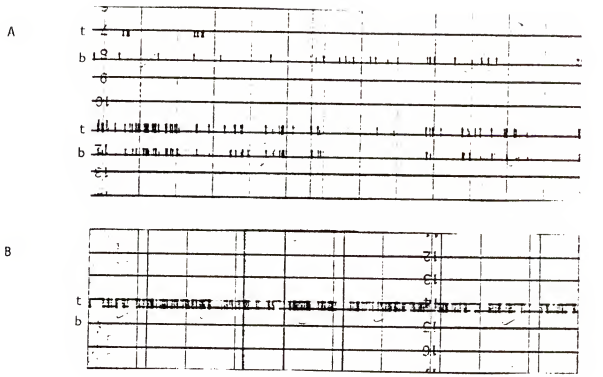


Figure 5. Segments of the event recorder record of swimming activity of green turtle hatchlings. Fifteen centimeters of tape record corresponds to one hour.

A. Casual swimming in two three-month old hatchlings.

B. Swimming frenzy activity in an eight-day old hatchling.

t Record from upper paddle
b Record from lower paddle

(obtained from values given only at certain points). A continuous time series, such as the event recorder records of turtle activity, may be analyzed either in a continuous (analog) or a discrete (digital) fashion. Data for discrete analysis may be obtained by sampling a continuous series at, or over, equal intervals of time. The latter procedure was used here so as to incorporate all relevant data, and discrete analysis allowed the use of a digital computing device (see Appendix 1).

Event recorder tape records were subdivided into 10 minute segments and data were recorded on coding sheets as the percentage of one hour that the turtle was active during each 10 minute interval for the duration of the experiment. This constituted the activity index. Activity during the feeding times when the turtles were absent from their recording tanks was coded as 0%. Since feeding hours were randomized during the photophase and the turtles could not predict them, the low activity levels did not bias the overall picture of the activity rhythm. The same was true for any change in activity level caused by aperiodic accidental disturbance of the turtles by other users of the room. I was not aware of any periodic accidental disturbance that might have affected the turtle's activity.

It was of primary importance that the discrete time series used in the covariance analyses should contain all the information present in the continuous time series from which it was derived. Initial observation of isolated turtle hatchlings showed that their daytime activity consisted of short bursts of activity alternating with total quiescence. Definition of any ultradian rhythms present in the hatchling activity pattern required the choosing of sampling intervals

narrow enough to allow isolation of the rhythms by covariance and spectral analysis. Statistically, the shortest periodicity (τ) that could be identified from the 10-minute sampling interval (Δ) was 20 minutes. For clarification refer to Appendix 1.

I considered this the shortest periodicity I could attempt to isolate on the basis of the accuracy and sensitivity of the recording apparatus and my own preliminary visual interpretation of the data. A 10-minute sampling interval and the BMD 02T program (Dixon 1971) limitation of 199 lags allowed the analysis of approximately seven days data at once. Longer periods were analyzed by extending the sampling interval to 30 or 60 minutes, or by sequentially analyzing seven-day blocks of data.

Analytical methods other than those normally involved in time series analysis were also frequently used to assist in the exact definition of the circadian rhythm and free-running period (FRP). These are described in Snedecor and Cochrane (1967) and Sokol and Rohlf (1969) and their use has been indicated where appropriate.

THE SWIMMING FRENZY

The mysterious "lost year," during which the whereabouts of neonate green turtles is largely unknown, is preceded by a dash from the nest to the sea and a period of frantic swimming, the infantile frenzy (Carr 1962, 1972). The function of this activity has not yet been demonstrated, but it is thought to assist in predator avoidance and to insert the young turtles into an offshore current system (Pritchard 1976) where they passively drift, probably in association with Sargassum rafts (Witham 1976, Fletemeyer 1978, Carr and Meylan personal communication), for the first year of their lives.

The features of the movement from nest to ocean have been thoroughly documented (for example, see Mrosovsky and Carr 1967, Mrosovsky and Shettleworth 1968, 1974, Philibosian 1976, Mrosovsky 1977, 1978), but the nature of the swimming frenzy is still the subject of much discussion. A group of captive green turtle hatchlings will, during the daylight hours, swim constantly and congregate at the walls of the brightest part of their tank (Carr 1962, 1965); this usually corresponds to the ocean side if the tank is near the sea. They will continue to swim in this fashion for several hours, perhaps days, until activity becomes random in direction and much reduced.

The swimming frenzy, if it does indeed serve to conduct the young to appropriate longshore currents, represents an important part of their life history and deserves further study. Frick (1976) tracked several hatchlings from the point of their first entry into the sea, but achieved

only limited success in determining the duration of the frenzy and the eventual position reached by the young turtles when the frenzied swimming subsided. The young were extremely hard to track and most were lost before they had traveled 2 km. Other information on the behavior of hatchling sea turtles in their natural environment is sparse, and casual observations on groups of young confined to tanks are of little value; young sea turtles in the ocean apparently swim well out of sight of others of their kind and do not rely on social cues for their behavior.

The present study was undertaken to determine, in a controlled laboratory environment, the exact nature and duration of the swimming frenzy of individual hatchlings, in hopes that the information gathered would allow an educated guess regarding the form and function of the frenzy in a natural situation.

Procedure

Hatchlings, in groups of five, were transported in a moist light-tight styrofoam container to the experimental room. They were then left for a minimum of two hours to allow partial acclimation to the warmer ambient temperature. Each turtle was then placed on a damp paper towel which was held slanted into the water of a swimming channel. Experiments involving pairs of turtles required simultaneous release of the turtles into different parts of the channel. The young could thus progress, in a somewhat normal fashion, into their "ocean." The actual entry, plus a minimum of five days subsequent activity, was recorded for investigation of the duration and characteristics of the juvenile swimming frenzy. The records of these naive turtles were

often extended beyond five days in order to examine the development of a mature activity pattern.

Introductions to the water were made during either the photophase or the scotophase, and hatchlings were exposed to various photoperiods as noted in Table 1. Photoperiods of 12L12D or 13L11D corresponded closely to those at latitudes of Tortuguero and Ascension Island (10°N and 7°S, respectively) where the turtles would normally emerge (Beck 1968). Twilights of 30 minutes also approximated the civil twilight duration at those latitudes. No attempt was made to regulate scotophase light intensities according to lunar phase or to vary the twilight spectral distribution in accordance with natural conditions.

The activity of healthy naive (to LD cycle and water) turtles of progressively increasing ages (6, 7, 8 and 10 days) was recorded in an attempt to determine the duration of the infantile frenzy "critical period." Turtles from the holding tanks that had been introduced to water at the age of 5 days were also tested to examine the effect of a novel environment (isolation and the swimming channel) on activity, and turtles in pairs were tested for analysis of the effect of social facilitation on activity patterns and frenzy duration.

Cumulative levels of activity (top plus bottom records) were compared by means of a Student's t-test (Snedecor and Cochrane 1967) after suitability of the data for comparison had been determined by an F-test. This gave a reasonable means of comparing turtles in different situations in spite of the slight differences in sensitivity among the tanks. All records were subjected to autocovariance and power-spectral analysis, and 80% confidence intervals were calculated

Table 1. Summary of swimming frenzy experiments. L and S refer to the large and small size classes of Tortuguero hatchlings. N refers to turtles naive to any LD cycle and to water; E indicates that experienced hatchlings were used. All times are given as local standard time (LST). Twilight consisted of 30 minutes of reduced light intensity (100 lux) at each end of the photophase. In all studies, full light commenced at 0800 LST. Where more than one experimental onset time is given, the experimental animals were evenly distributed among the experimental situations. Numbers of turtles tested are denoted by n.

Source of Turtles	Age in Days	n	Photoperiod	Twilight	Time of Onset	Remarks
Tortuguero	5	$15_N^{4L,11S}$	LD12:12(270:0.1)	+	0230, 1000, 2200	
	5	$8_N^{1L,7S}$	LD12:12(270:0.1)	-	0300, 1000	One record terminated on day 4 due to equipment failure; one turtle was eaten by an escaped lizard during the day 4 feeding session.
	5	$5_N^{2L,3S}$	LD13:11(270:0.1)	+	0300, 1600	
	5	$10_N^{2L,8S}$	LL(270)	-	1000	
	5	6_N^{S}	LD12:12(270:0.1)	+	2200	Turtles tested in pairs.
	6	$10_{5N,5E}^{S}$	LD12:12(270:0.1)	+	2200	
	7	$5_{3N,2E}^{S}$	LD12:12(270:0.1)	+	2200	
	8	$5_{3N,2E}^{S}$	LD12:12(270:0.1)	+	2200	

Table 1. continued.

Source of Turtles	Age in Days	n	Photoperiod	Twilight	Time of Onset	Remarks
Tortuguero	10	$5^{S}_{3N,2E}$	LD12:12(270:0.1)	+	2200	
	10	4^{S}_{N}	LD13:11(270:0.1)	-	2200	One record terminated day 3 due to equipment failure.
	10	$5^{S}_{3N,3E}$	LL(270)	-	2200	
	10	$6^{S}_{4N,2E}$	LD12:12(270:0.1)	+	2200	Turtles tested in pairs.
Ascension Island	5	7_{N}	LD12:12(270:0.1)	+	0300, 1000, 2200	Three records terminated day 4 due to equipment failure.
	5	10_{N}	LD12:12(270:0.1)	-	0300, 1000	
	5	8_{N}	LL(270)	-	1000	Two records terminated day 4 due to equipment failure.
	5	6_{N}	LD12:12(270:0.1)	+	2200	Turtles tested in pairs.
	6	$5_{3N,2E}$	LD12:12(270:0.1)	+	2200	
	7	$5_{3N,2E}$	LD12:12(270:0.1)	+	2200	
	8	$10_{5N,5E}$	LD12:12(270:0.1)	+	2200	

Table 1. continued.

Source of Turtles	Age in Days	n	Photoperiod	Twilight	Time of Onset	Remarks
Ascension Island	10	$9_{5N,4E}$	LD12:12(270:0.1)	+	2200	One record terminated day 3 due to equipment failure.
	10	$7_{3N,4E}$	LL(270)	-	2200	Three records terminated (one day 3, two day 4) due to equipment failure.
	10	$6_{4N,2E}$	LD12:12(270:0.1)	+	2200	Turtles tested in pairs.
Galapagos Islands	13	1_E	LD12:12(270:0.1)	+	2000	
	19	2_E	LD12:12(270:0.1)	+	2000	
	24	1_E	LD12:12(270:0.1)	+	2000	
	19,36	$1_E, 1_E$	LD12:12(270:0.1)	+	2000	Turtles tested as a pair.

for all spectral-density estimates. Some records were compared to themselves at different times and to others by crosscovariance analysis. To the extent possible (the number of turtles available was extremely limited) hatchlings of both large and small size classes from Tortuguero were tested.

All activity records were visually examined for evidence of a swimming frenzy. The data were then combined to give a total activity level for each full photophase and each scotophase. Continuous light activity records were summed over 12-hour intervals.

The length of the frenzy was defined as the number of days (dawn to following dawn) that the photophase and/or the 24-hour activity level was significantly greater ($p < 0.5$) than the stable level attained by the end of the 5-day test. Preliminary observations indicated that no frenzy activity extended beyond 5 days. Twenty-four hours of activity, with a lag of 12 hours, were compared for activity records collected under LL. The shape of the activity plot was also examined to determine the nature of the frenzy. For example, in many cases the responsiveness of the turtle to the transition from dark to light changed at the end of the swimming frenzy. The information gained was used in conjunction with the statistical analyses to give a rough estimate (days rather than hours or minutes) of the frenzy duration. It is doubtful that a more precise estimate would be possible or if one would be of any greater use as an indicator of the ecologic function of the juvenile frenzy. Average activity indices were calculated for each 24 hours during the frenzy. They were also calculated for each photophase (l) and for each scotophase (d). The numbers of active (α) and passive (ρ) hours

in each 24-hour period were determined. Each hour with a cumulative activity index greater than the mean was defined as an active hour.

Results

The individuality demonstrated by green turtle hatchlings must be emphasized at the outset, but in spite of this variability many generalizations regarding their activity patterns are possible.

Tortuguero Hatchlings

Naive turtles

All hatchlings first exposed to water during the scotophase showed an initial high level of activity (9 to 23 min/hr) which gradually declined toward the first dark-light interface. Bursts of swimming activity alternated with periods of rest. An increase in swimming activity to a level higher than any seen to that point occurred during the first dawn in all but one turtle. The one exception showed the same pattern but exhibited lower overall activity levels. The form and amplitude of the increase was the same whether or not a twilight phase was present. Figure 6 shows two typical activity records of a scotophase entry and the subsequent swimming frenzy. The marked response to an increased light intensity continued for the duration of all the experiments. The amplitude of activity gradually declined until a stable pattern and amplitude marked the end of the frenzy as I have defined it.

The swimming frenzy lasted for from two to four days in Tortuguero hatchlings of the small size class (see Table 2 for sample values).

Figure 6. The swimming frenzy of two Tortuguero hatchlings of the small size class first exposed to water during the scotophase.
LD+t13:11(270:0.1)

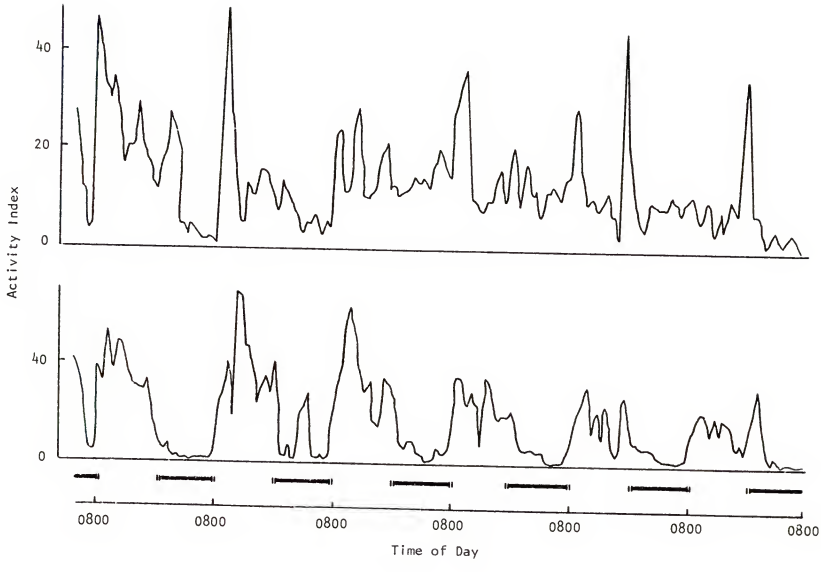

40
20
0
Activity Index
40
0
0800
0800
0800
0800
0800
0800
0800
Time of Day

Table 2. Swimming frenzy activity levels of two representative small size class hatchlings from Tortuguero, Costa Rica. Turtle A showed a four-day frenzy, turtle B showed a three-day frenzy. Both were five days old and naive to water and an LD cycle at the start of the experiment. LD13:11(270:0.1)

	Day	Average Activity Index/24 Hours	Average l	Average d	Average $s(\alpha)$	Average $r(\rho)$	$\frac{l}{d}$	$\frac{\alpha}{\rho}$
A	1	13.08 ±10.36	24.27 ±6.60	8.64 ±9.12	24.79 ±5.65 (14)	6.39 ±5.39 (10)	2.81	1.40
	2	13.02 ±9.88	17.88 ±11.08	7.27 ±3.74	19.05 ±9.06(8)	6.17 ±5.06(16)	2.46	0.50
	3	15.63 ±8.72	15.50 ±5.71	15.77 ±5.93	16.62 ±5.82(7)	5.99 ±4.79(17)	0.98	0.41
	4	15.06 ±9.01	16.62 ±9.31	13.23 ±4.33	16.95 ±8.24(7)	6.25 ±4.77(17)	1.26	0.41
	5	11.04 ±6.79	12.88 ±7.42	8.86 ±5.37	13.11 ±6.57(7)	5.37 ±3.92(17)	1.45	0.41
	6	7.92 ±7.81	11.50 ±10.12	3.68 ±1.42	12.80 ±5.94(10)	4.58 ±1.61(14)	3.12	0.71
	11	8.73 ±9.19	15.46 ±7.37	0.77 ±1.44	16.71 ±4.76(11)	1.88 ±2.79(13)	20.01	0.85
B	1	20.25 ±18.58	35.40 ±13.24	2.50 ±2.36	35.93 ±7.57(12)	5.18 ±6.33(12)	14.17	1.00

Table 2. continued.

	Day	Average Activity Index/24 Hours	Average l	Average d	Average α	Average α	l/d	α/ρ
B	2	25.56 ±12.03	37.73 ±12.71	11.18 ±2.37	36.03 ±6.94(14)	5.13 ±5.09(10)	3.37	1.40
	3	21.90 ±6.59	36.04 ±11.65	5.18 ±2.49	33.04 ±7.01(10)	5.21 ±4.73(14)	6.96	0.71
	4	16.63 ±8.53	26.73 ±10.34	4.68 ±3.26	24.91 ±6.82(12)	5.17 ±3.00(12)	5.90	1.00
	5	12.14 ±9.66	19.27 ±9.17	4.59 ±3.34	16.99 ±4.10(11)	5.02 ±2.98(13)	4.20	0.95
	6	12.54 ±10.36	16.81 ±8.94	4.73 ±4.42	17.03 ±3.02(13)	4.78 ±2.64(11)	3.56	1.18
	11	14.96 ±13.68	23.62 ±14.72	4.59 ±2.38	25.73 ±5.91(11)	5.84 ±2.68(13)	5.15	0.85

Only one turtle showed no frenzy activity. The majority (90%) showed a three-day frenzy. The distribution of swimming during the frenzy seemed to be an individual characteristic, but in all cases the major activity was concentrated in the photophase (Table 2).

All the five-day-old hatchlings of the large size class (Fig. 7) had a frenzy of shorter duration than that of the small size class turtles, lasting only two days. The frenzy pattern was also somewhat different, with the initial daylight activity levels similar to those seen when the stable post-frenzy swimming pattern developed. The average amount of activity also appeared lower than that of the small hatchlings. Activity levels on their second day in the water were always among the lowest recorded for these turtles. Examination of the shape of the frenzy activity plot was vital here to the determination of duration, as 24-hour activity levels did not change significantly with time. An increase in the degree of diurnalism (measured by I/d) marked the end of the frenzy. Sample calculations of activity levels are shown in Table 3.

The frenzy pattern and duration were apparently not a function of age in turtles younger than 10 days. The 10-day-old naive turtles, however, showed nothing that could be interpreted as a swimming frenzy. Changing the time of introduction to water from the scotophase to the photophase had no observable effect on the frenzy activity. There were no apparent differences in the behavior of turtles collected in the three different years.

Naive hatchlings introduced to water under an LL photoperiod showed activity patterns typified by those depicted in Fig. 8. All

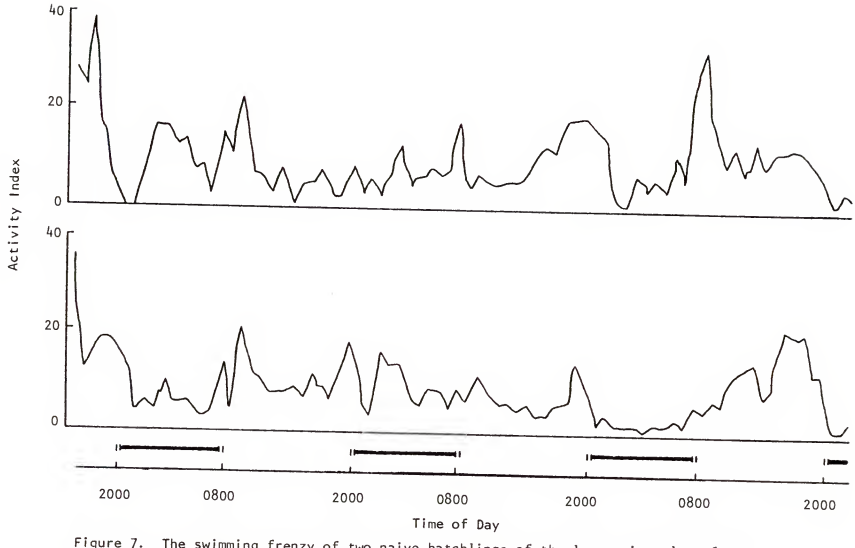
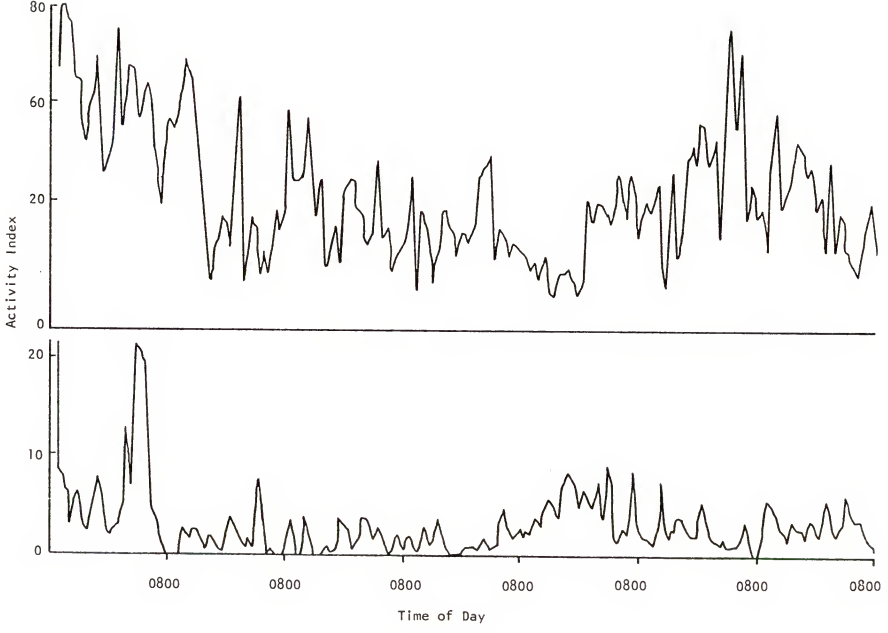


Figure 7. The swimming frenzy of two naive hatchlings of the large size class from Tortuguero, Costa Rica.
LD+t13:11(270:0.1)

Table 3. Swimming frenzy activity levels of two representative naive Tortuguero hatchlings of the large size class (A and B). Both had swimming frenzies of two days duration.
LD+t13:11(270:0.1)

	Day	Average Activity Index/24 Hours	Average l	Average d	Average s(α)	Average r(ρ)	$\frac{l}{d}$	$\frac{\alpha}{\rho}$
A	1	11.79 ±9.50	13.35 ±11.56	9.95 ±5.85	20.70 ±7.87(10)	5.43 ±3.55(14)	1.34	0.71
	2	6.92 ±3.34	6.31 ±2.53	7.64 ±4.08	9.45 ±3.24(11)	4.77 ±1.30(13)	0.83	0.85
	3	11.38 ±7.61	14.31 ±6.68	7.91 ±6.93	17.91 ±5.84(11)	5.85 ±3.21(13)	1.81	0.85
	5	11.02 ±6.91	14.27 ±5.94	7.43 ±6.24	17.22 ±5.82(11)	5.76 ±2.97	1.92	0.85
B	1	11.42 ±7.85	14.92 ±9.09	7.27 ±5.71	18.70 ±7.01(10)	6.21 ±2.22(14)	2.05	0.71
	2	8.17 ±3.68	7.31 ±3.62	9.18 ±4.58	12.00 ±3.12(9)	5.87 ±1.25(15)	0.80	0.60
	3	8.13 ±6.75	12.73 ±6.08	2.68 ±2.10	15.67 ±4.47(10)	3.60 ±2.23(14)	4.75	0.71
	5	8.15 ±4.33	11.21 ±4.28	3.02 ±1.97	14.76 ±3.02(11)	3.57 ±2.96(13)	3.71	0.85

Figure 8. The swimming frenzy of two representative hatchlings of the small size class from Tortuguero, Costa Rica. LL(270)


80
60
20
0
Activity Index
20
10
0
0800
0800
0800
0800
0800
0800
0800
Time of Day

hatchlings, regardless of size or time of entry into the water, showed initial high levels of activity followed by a gradual decline marked by short bursts of swimming. The swimming frenzy corresponded closely to the duration of this decline and was generally shorter in LL than in LD, lasting only a day in 50% of the turtles and two days in the rest (Table 4). The overall time spent swimming during the LL frenzy, however, was only slightly less than that spent under LD conditions, although the difference was significant at $p < 0.5$.

Only two naive large hatchlings were tested under LL conditions, so it is almost impossible to make a valid comparison of their frenzy durations with those of the small turtles. The data collected show that their average frenzy duration was less than that under LD but that the average activity levels were the same.

Experienced turtles

Turtles which had been initially introduced to water and an LD cycle at the age of five days in the holding tanks (a social environment) and then transferred to the recording tanks behaved as expected for hatchlings of their age, which was estimated by extrapolating their weight and carapace lengths onto the growth curve calculated for the turtles reared in the experimental tanks. The age estimate for turtles 10 days old and younger was probably reliable, as the major slowing of growth of the holding tank turtles did not appear until the age of approximately 15 days. No frenzy activity was recorded for 10-day-old hatchlings, and for those younger than 10 days, the recorded frenzy shortened with age. The novel environment in the recording room (new tank, sudden isolation and warmer ambient temperature) apparently had

Table 4. Representative samples of the total activity time (in hours) during the swimming frenzies of turtles maintained under LL and LD photoperiods. Data gathered for Tortuguero hatchlings of both small and large size classes are presented. Total activity represents the summed activity indices for all hours whose average activity index was greater than that of the mean for the day.

Hatchling Class	LD		LL	
	Activity Time in Hours	Frenzy Duration in Days	Activity Time in Hours	Frenzy Duration in Days
Small	7.34	4	7.59	2
	8.78	3	8.46	2
	12.66	3	7.61	2
	9.04	3	1.31	1
	8.39	3	3.42	1
	Overall average activity time = 9.43 ± 4.22 hours		Overall average activity time = 5.47 ± 4.07 hours	
Large	2.95	2	4.06	2
	3.11	2	3.17	1
	Overall average activity time = 3.03 ± 0.08 hours		Overall average activity time = 3.62 ± 0.45 hours	

no effect on the activity pattern. The form of the frenzy was the same in all experimental situations as that of the naive hatchlings.

Paired turtles

Placement of hatchlings in pairs in the recording tanks resulted in an increase in activity levels of approximately 32% during the photophase, but no change in scotophase activity occurred. This was probably the result of mutual jostling, which I saw many times. No change in the duration or form of the frenzy was seen. The turtles did, however, appear more continually active than isolated hatchlings, probably due to social facilitation.

Ascension Island Hatchlings

Naive turtles

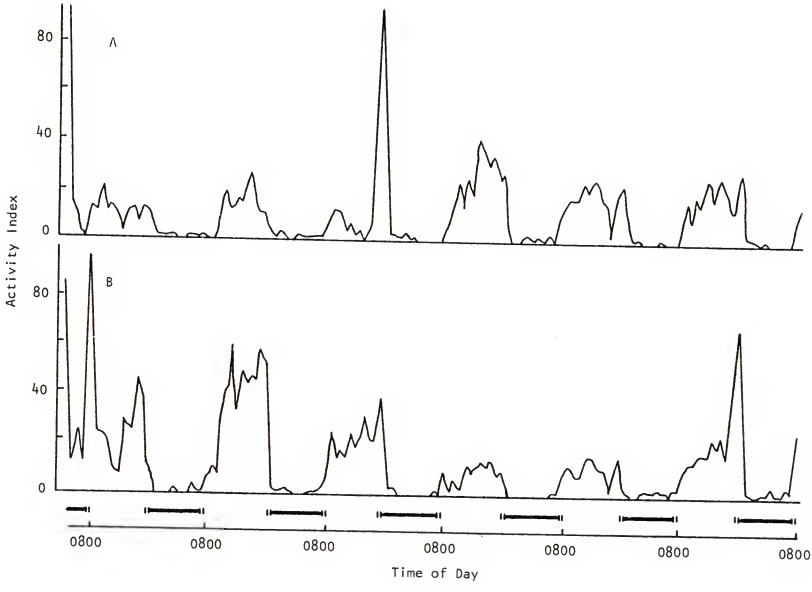
Eleven (64.7%) of the 17 hatchlings tested under LD conditions showed no swimming frenzy activity beyond a one-hour peak after first exposure to water (Fig. 9A). The remaining six turtles showed a frenzy typified by Fig. 9B. All these hatchlings had a two-day frenzy, and the average swimming time during this frenzy was 8.27 ± 3.29 hours, not significantly different ($p < 0.5$) from that spent swimming by the small Tortuguero turtles (9.43 ± 4.22 hours). The swimming was, however, concentrated over a shorter time (two rather than three days) and was differently distributed, with a greater degree of diurnalism evident throughout.

All other characteristics of the swimming frenzy of these Ascension Island hatchlings were remarkably similar to those of turtles from Costa

Figure 9. Swimming frenzy of two naive hatchlings from Ascension Island.

A. No swimming frenzy evident.
B. Swimming frenzy of two days.

LD+t12:12(270:0.1)


A
B
80
40
0
Activity Index
0800
0800
0800
0800
0800
0800
0800
Time of Day

Rica. The presence or absence of twilight had no observable effect on frenzy duration, and no turtles over the age of eight days showed activity which could be classified as a swimming frenzy. Likewise, the time of entry into the water (photophase or scotophase) had no apparent effect on frenzy duration.

Under continuous light, the eight hatchlings showed frenzy patterns typified by Fig. 10. Four showed no frenzy activity, and four underwent a short frenzy lasting two days. The average active swimming time of the latter four was 21.94±7.68 hours, much longer than that of the small or large Tortuguero hatchlings (5.47±4.07 and 3.62±0.45, respectively).

Experienced turtles

Again, the Ascension Island hatchlings reacted in a similar fashion to those from Tortuguero. Four of the nine six- to eight-day-old green turtles showed no frenzy activity, although it was impossible to know whether they had exhibited a frenzy while in the holding tanks. The remainder behaved as if they had been in the recording tank from the start and recording of activity had commenced part way through the frenzy. No 10-day-olds showed frenzy activity, regardless of photoperiod.

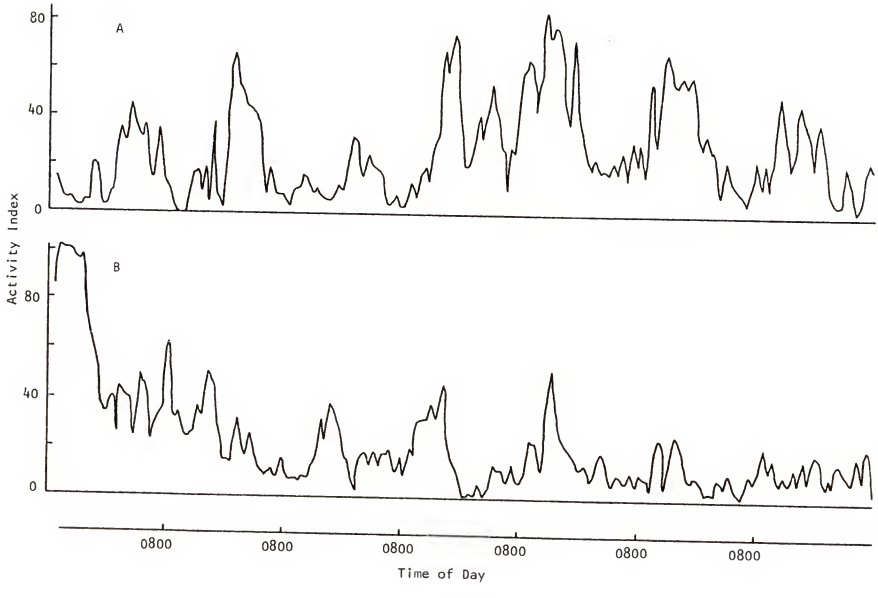
Paired turtles

Testing again resulted only in an average elevation of photophase activity levels (approximately 28%); no effect on frenzy duration was noted.

Figure 10. The swimming frenzy of two representative naive hatchlings from Ascension Island.

A. No swimming frenzy evident.
B. Swimming frenzy of two days.

LL(270)


A
B
80
40
0
80
40
0
Activity Index
0800
0800
0800
0800
0800
0800
Time of Day

Galapagos Islands Hatchlings

All of these turtles had been exposed to water and an LD cycle by the time they became available for testing. The only one to show possible frenzy activity was the 13-day-old (Fig. 11A). Its elevated activity lasted one day and was marked by high nocturnal activity levels and a decline during the first photophase. All of the other hatchlings showed an activity pattern typified by Fig. 11B. They exhibited no frenzy other than a one-hour activity burst following entry into the swimming channel which perhaps represented a predator-escape reaction. They also showed a strong depression of swimming activity during the scotophase.

Discussion

Analysis of swimming frenzy records revealed distinct differences among the groups of hatchlings studied. The activity, as it was recorded and analyzed in the laboratory, must be assumed to be representative of that which would occur in a natural situation if any discussion of the ecologic effect of the swimming frenzy is to be of value.

There were, obviously, several distinctive features of the laboratory environment which could have influenced hatchling behavior. There was no indication, however, from hatching success, weight, general appearance or elsewhere, that the young captive turtles were significantly less fit than turtles undergoing a natural hatching and emergence. Indeed, some recent studies (Hirth and Schaffer 1974, Witham and Futch 1977) indicate reasonably good survival rates in artificially incubated sea turtles.

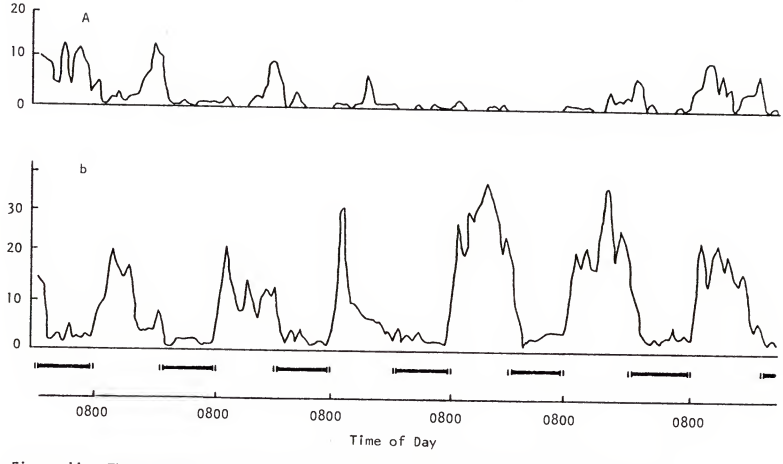


Figure 11. The swimming frenzy of two hatchlings from Galapagos Islands which had been previously exposed to water.

A. One day frenzy in a hatchling approximately 13 days of age.
B. No frenzy apparent in 24 day old hatchling.

LD+t12:12(270:0.1)

The mode of their release into the water could have posed a major difficulty if, as Frick (1976) suggests, the natural progression from nest to sea acts as a releaser of a series of ontogenetic orientation and swimming activities. The release from a paper towel could not possibly have duplicated the stimuli of the dash across the beach, but I observed none of the frantic activity Frick saw in turtles released directly into the sea, and therefore assume at least partial compensation for the natural progression.

The swimming channels also lacked any wave action which may stimulate a positive rheotactic response and possibly assist in the setting of an orientation preference. This did not apparently affect the activity of the hatchlings, but it may have resulted in a reduction of activity levels, especially just after initial entry into the water (equivalent to the passage through the surf), and may have affected direction preference, which was not under study here. I could think of no effective way to mimic wave action in the channels and simultaneously to record turtle activity by the recording method used.

All the young, as noted, began eating by their third day in the water at an age of eight days. This age corresponded closely with the cessation of frenzy activity. It also coincided with the closure of the umbilical scar and therefore with the complete utilization of the yolk sac food source. After yolk sac absorption, hatchling sea turtles must eat to survive and it seems likely that, energetically, they cannot afford to maintain frenzy activity beyond this time. Their activity levels must therefore be reduced and association with drifting Sargassum rafts would provide the food the carnivorous green turtle young require.

Examination of the swimming frenzy of turtles exposed to continuous light further corroborated the basic differences between the groups of hatchlings. Continuous light is not normally encountered by hatchlings and may have several potential effects on activity cycles and amplitudes (see review by Bünning 1973). The LL data, therefore, might not give a realistic picture of frenzy duration under normal LD conditions.

The results obtained, then, are probably a reliable representation of the natural swimming frenzy. Turtles from Ascension Island, the Galapagos, and the two size classes from Tortuguero, Costa Rica, have distinctive characteristics which, on the average, distinguish their swimming frenzies from all others. It is probable that these frenzy differences represent actual genetic differences between the populations from which the hatchlings were derived, differences which perhaps evolved in response to migration requirements. The existence of a swimming frenzy in turtles younger than 10 days, but older than 5 days, could reflect a "critical period" during which exposure to water will elicit a swimming frenzy response, thus allowing for some delay in the movement of hatchlings up to the beach surface and actual differences in hatching times within an individual nest.

It then becomes of interest to correlate the measured duration of the frenzy and the activity levels shown with the environmental situation faced by young turtles off their nest beach. The popular theory of current-mediated dispersal (that is, that the young are planktonic for all or most of their first year of life) is in part based on the fact that the young turtles are too small and weak to do much to control their movements.

Fischer (1964) and Frick (1976) have both noted indications of a preferred compass direction in swimming hatchlings. Hatchlings on the beach show no compass preference (Carr and Ogren 1960), and the stimulation of water along with the direction of travel across the beach from nest to sea may help set a preferred swimming direction. Knowledge of this direction combined with that of the average swimming speeds of hatchling sea turtles (determined by Frick 1976) and the current speeds faced by the young when they undertake the swimming frenzy allow a rough calculation of the position gained by the young by the end of the juvenile frenzy.

Young sea turtles entering the ocean on a path roughly perpendicular (Carr 1972, Frick 1976) to their nesting beaches on Ascension Island are almost immediately immersed in one of the most stable current systems in the world. The South Equatorial Current maintains almost constant year-round temperatures and salinities (Anon. 1967) and has few variations in speed, averaging 1.3 km/hr, or pattern of flow toward the bulge of Brazil approximately 2000 km away, where it splits into north- and south-trending components (Anon. 1955).

Hatchlings leaving the nesting beaches on the west coast of the island should not need a long period of frenzied swimming to reach the prevailing current and be swept toward Brazil. In their case, the primary purpose of any frenzy might only be to pass through the surf and not be swept back up on the beach. There is no possibility that the frenzy could carry them to any other than the South Equatorial Current.

Hatchlings entering the waters off Tortuguero, however, face a potentially more complex situation, especially if they have inherited

a tendency to position themselves in a specific current system by controlling the duration of their swimming frenzy. Such a tendency might allow them to control the direction of their passive drift, but it assumes genetic separation of breeding adults from feeding grounds to the north and south of Tortuguero, which has not been proven.

Drift bottle experiments (Carr 1972) show that the currents off the north-east segment of the Tortuguero nesting beach could potentially carry hatchlings to the feeding grounds off Nicaragua and Colombia. The longshore current off Tortuguero is south-trending overall, averaging 0.65 to 0.88 km/hr (Frick 1976, Meylan 1978), but it is highly variable and occasionally reverses direction completely. Farther offshore (at least beyond two kilometers) the southeast-trending current is steadier at approximately 1.85 km/hr (Anon. 1955) and if the turtles can reach this region, it can be assumed that they are carried to the southeast of their nesting beach.

The hatchlings which Frick (1976) tracked off Tortuguero and Bermuda averaged swimming speeds of 1.5 km/hr. If one assumes a hatchling were attempting to maintain a swimming direction perpendicular to the shore (approximately a 60° heading off Tortuguero) it would be crossing a current averaging 1.85 km/hr flowing at right angles to its desired line of travel. The current would have an approximate heading of 150° (Meylan 1978).

The Tortuguero hatchlings of the small size class had an average swimming frenzy of three days, during which they actively swam an average of 9.43 hours. At the end of their frenzy, then, they could be expected to be 133.18 km downstream from their point of entry and approximately 13.72 km offshore.

The large hatchlings, however, averaged only a two-day frenzy with 3.03 hours of strong swimming. Using the swimming speeds reported by Frick (1976) I calculated their possible location at the end of the frenzy as 88.79 km downstream and only 4.54 km offshore.

If post-frenzy activity is not oriented to a particular compass direction and the young passively drift with the currents on sargassum rafts, then examination of the prevailing current patterns at the times of year the swimming frenzy subsides should allow a prediction of the eventual fate of the hatchling.

During the peak hatching months at Tortuguero, September through November, the southeast-trending current flows at 1.85 km/hr along the shore to approach closely off Colón, approximately 400 km downstream from Tortuguero. In September it slows and swings offshore from Cartagena (Anon. 1955) to form a counterclockwise gyre meeting the west-trending North Equatorial Current. There is also a weak (less than 25% stable) offshore current from Colón forming a tighter gyre to meet the North Equatorial Current.

By October, the current off Tortuguero has strengthened to approach 50 to 100% stability and the gyre off Colón is stronger and more stable, although the North Equatorial Current has moved farther offshore. The branch to Cartagena is stronger and now splits to give a flow toward Punta Gallinas as well as toward the North Equatorial Current.

November sees a reduction in the stability, to between 25 and 50%, but not in the speed of the Tortuguero current, and the loss of the Colón gyre. There is also a weakening of the North Equatorial Current-trending flow off Cartagena. By the end of the hatching season in

December there is no current flow to Cartagena. The Tortuguero current swings out at Colón, and the North Equatorial Current makes a strong inshore sweep by Punta Gallinas and Cartagena. It then swings offshore at Colón. After this time, from January to April, any hatchling drifting off the Tortuguero beach would face a closed counterclockwise gyre which might completely prevent it from reaching the North Equatorial Current.

One can argue that the farther offshore a hatchling gets during its swimming frenzy, the greater the chance of its being caught up in the gyre leading to insertion in the North Equatorial Current, and possibly to the area of Nicaraguan feeding grounds. Those remaining close to shore (the larger size class) might tend to remain in the longshore flow toward Cartagena and the Colombian feeding grounds. Both arguments require, however, that the turtles be drifting at a time when the "desired" currents are present, if it is their "goal" to drift to the feeding grounds of their parents. The timing of a female's laying might therefore influence the eventual fate of her young. If, for example, a hatchling emerges early in the season (September or October), it stands an equal chance, depending on the distance it swims offshore, of gaining access to the North Equatorial Current, and Nicaragua, or Colombia. In November it would be more likely to remain in Colombian waters regardless of how far offshore it tried to swim, and in December its only possible fate would be to meet the North Equatorial Current and move west.

Carr and his coworkers (1978) report the peak laying months at Tortuguero as August and September, with 75% of the Nicaraguans and 63.9% of the Colombians arriving early in July and 20.5% of the

Nicaraguans and 36.1% of the Colombians arriving in September. This means that more northern than southern hatchlings might emerge in September, while the reverse would be true in November. This would be an interesting coincidence, if nothing more, for there are no data to indicate that hatchlings are found on the adult feeding grounds. There is a good chance that the young are instead carried on their sargassum rafts beyond the feeding grounds and perhaps into the Sargasso Sea. If so, another coincidence should be mentioned. The Tortuguero young drifting north could be expected to reach the southern boundary of the Sea from January to March. At this time of year, the Sargasso gyre is warm enough (around 25°C) to allow optimal turtle activity, and a hatchling entering the gyre and circling with it for its 11 month cycle time (Weyl 1978) would experience no significant temperature changes. At any other time of year, a hatchling entering the south side of the gyre would be exposed to very low temperatures in parts of the circuit.

It should finally be noted that most of the Tortuguero young of the small size class that were used in this study hatched in late October and the first week of November. They probably represented young primarily from the Nicaraguan population.

TEMPORAL PATTERNS OF LOCOMOTOR ACTIVITY

Considerable effort has been devoted to the laboratory and field study of biological rhythms and to the entrainment of activity rhythms by light-dark cycles, but most of the work has concentrated on the behavior of mammals, birds, and insects (see reviews by Bünning 1973, and by Dann and Aschoff 1975). A small number of reviews of endogenous behavioral rhythms in fish are available (Schwassmann 1971b, Richardson and McCleave 1974), as are some on amphibians and reptiles (see Bünning 1973). The limited data and interpretations provided make it difficult, however, to say whether these animals share the properties described for vertebrate circadian rhythms as derived from the studies on homeotherms.

Fischer (1964) achieved a phase-shifted orientation response to solar cues by hatchling green turtles. The response was indicative of a biological time sense, usually accepted as one of the overt expressions of an endogenous rhythm. A precise time sense would be useful during migration, if it were used as the basis for time-compensated sun-compass orientation. In order to corroborate the existence of an endogenous rhythm in sea turtles, I undertook an investigation of the characteristic patterns and circadian aspects of the swimming activity of hatchling green turtles from Tortuguero, Costa Rica, and Ascension Island.

Table 5 provides a summary of the turtles studied and the conditions of photoperiod to which they were exposed. The present study

Table 5. Summary of the experiments performed to determine the temporal patterns of swimming activity in hatchling green turtles. Number of turtles is denoted by n.

Source of Turtles	n	Approximate Age at Onset of Experiment in Days	Photoperiod	Twilight	Duration of Experiment in Days	Remarks
Tortuguero	10	10	LD12:12(270:0.1)	+	12 - 20	Continuation of swimming frenzy experiment
	5	16 - 30	LD12:12(270:0.1)	+	7	
	5	10 - 30	LD12:12(270:0.1)	-	7	Four were extensions of frenzy experiments
	5	10 - 30	LD13:11(270:0.1)	+	7	Five were extensions of frenzy experiments
	5	16 - 30	LD13:11(270:0.1)	-	7	
	5	31 - 45	LD12:12(270:0.1)	+	7	
	4	46 - 100	LD12:12(270:0.1)	+	7	
	5	100 - 150	LD12:12(270:0.1)	+	7	
	5	56	LD12:12(270:0.1)	+	5	
			LL(270)	-	30	
			LD12:12(270:0.1)	+	10	
	5	68	LD12:12(270:0.1)	+	14	
			LL(270)	-	24	
			LD12:12(270:0.1)	+	5	
	5	92	LD12:12(270:0.1)	-	7	
			LL(270)	-	29	
			LD12:12(270:0.1)	-	5	
	5	113	LD13:11(270:0.1)	+	25	
			LL(270)	-	30	
			LD13:11(270:0.1)	+	5	

Table 5. continued.

Source of Turtles	n	Approximate Age at Onset of Experiment in Days	Photoperiod	Twilight	Duration of Experiment in Days	Remarks
Tortuguero	5	157	LD13:11(270:0.1)	-	25	
			LL(270)	-	29	
			LD13:11(270:0.1)	-	5	
Ascension Island	5	10	LD12:12(270:0.1)	+	25	Continuation of swimming frenzy experiment
			LL(270)	-	30	
			LD12:12(270:0.1)	+	5	
	5	39	LD12:12(270:0.1)	-	25	
			LL(270)	-	30	
			LD12:12(270:0.1)	-	5	
Galapagos Islands (Pacific Black Turtles)	5	30	LD12:12(270:0.1)	+	10	Continuation of swimming frenzy experiment
Tortuguero	5	55	LD12:12(270:0.1)	+	5	
			LD14:10(270:0.1)	+	6	
			LD16:8(270:0.1)	+	17	
			LD18:6(270:0.1)	+	17	
			LD20:4(270:0.1)	+	15	
			LD22:2(270:0.1)	+	7	
			LL(270)	-	10	
			LD18:6(270:0.1)	+	7	
			LD12:12(270:0.1)	+	5	

Table 5. continued.

Source of Turtles	n	Approximate Age at Onset of Experiment in Days	Photoperiod	Twilight	Duration of Experiment in Days	Remarks
Tortuguero	5	78	LD12:12(270:0.1)	+	10	
			LD12:12(270:0.1)	+	15	Phase advance of 3 hours
			LD12:12(270:0.1)	+	8	Phase delay of 3 hours
		121	LD12:12(270:0.1)	-	9	
			LD12:12(270:0.1)	-	12	Phase advance of 3 hours
			LD12:12(270:0.1)	-	7	Phase delay of 3 hours

was an attempt to: 1) determine the temporal distribution of swimming activity in a photoperiodic and thermal environment approximating the natural environment of hatchling sea turtles; 2) define the extent to which the timing of swimming activity is circadian and under endogenous control; and 3) conduct a preliminary investigation into the nature of that control.

Temporal Distribution of Activity Under Natural Light-Dark Cycles

Study of the circadian nature of periodic activity of an animal requires an initial description of that activity under photoperiodic conditions normal to that animal. This section provides such a description. It also provides a detailed laboratory-based analysis of the activity patterns of an animal, the young green turtle (and the Pacific black turtle), that has rarely been found and studied in its native environment.

Procedure

The experiments performed are summarized in Table 5. All turtles used were well past the swimming frenzy stage. Analysis of the temporal distribution of swimming activity under an LD cycle involved the following steps.

1) Breaking the record into 10-minute, 30-minute, and 60-minute intervals and plotting the activity indices for visual examination.
2) Plotting daily activity as the deviation from the average of three-hour moving means (this smoothed the record) for visual examination.

3) Standardizing the data over one week by dividing the summed activity index of each hour multiplied by 1000 by the total activity index for the week. The zero activity index obtained when the turtles were absent from their tanks during feeding was replaced by the average of the rest of the week's data for that particular hour. This allowed examination and comparison of the activity patterns without confusion from individual differences in activity levels.

4) Subjecting the activity records to autocovariance, cross-covariance and spectral analysis.

Results

Tortuguero hatchlings

The hatchlings from Tortuguero, under photoperiods of LD+t12:12 (270:0.1) and 13:11(270:0.1), showed a bimodal distribution of swimming activity with amplitude peaks in the photophase, coming well after full light and before the onset of dusk. Figure 12 shows the typical distribution of swimming activity over time exhibited by these turtles. Non-smoothed records showed much greater hour-to-hour variability and hence were extremely difficult to analyze. They have not been included here. The records once again illustrate considerable variability among the young sea turtles. Data were plotted as the deviation of three-hour average activity indices from the daily mean, and as such limit the use of the plots in identifying the abilities of the hatchlings to anticipate light-dark transitions.

Autocovariance analysis (Fig. 13) gave evidence of the 24-hour cycle of activity, but only hints of the bimodal distribution of swimming

Figure 12. Representative plots of the distribution of swimming activity over time in five green turtles from Tortuguero, Costa Rica. Data were plotted as deviations of three-hour moving means from the daily average activity index. Plot f represents the average of plots a through e.
LD+t13:11(270:0.1)

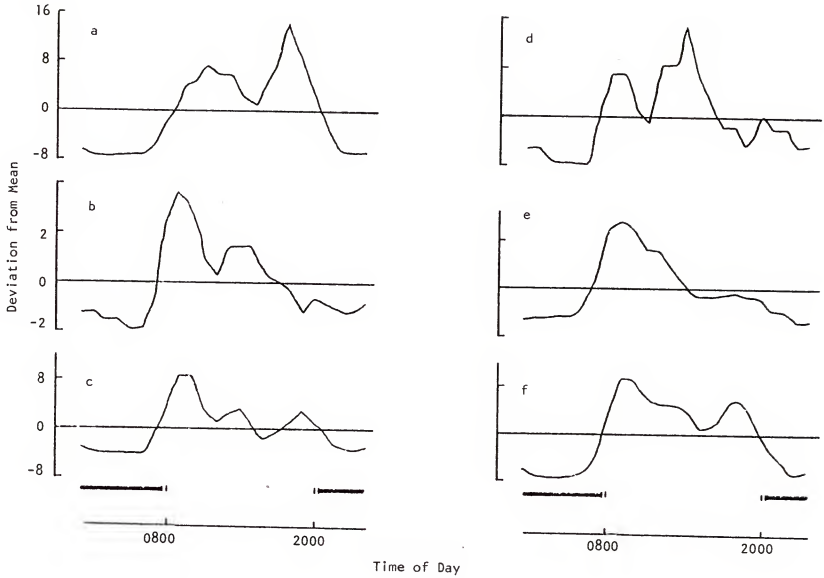
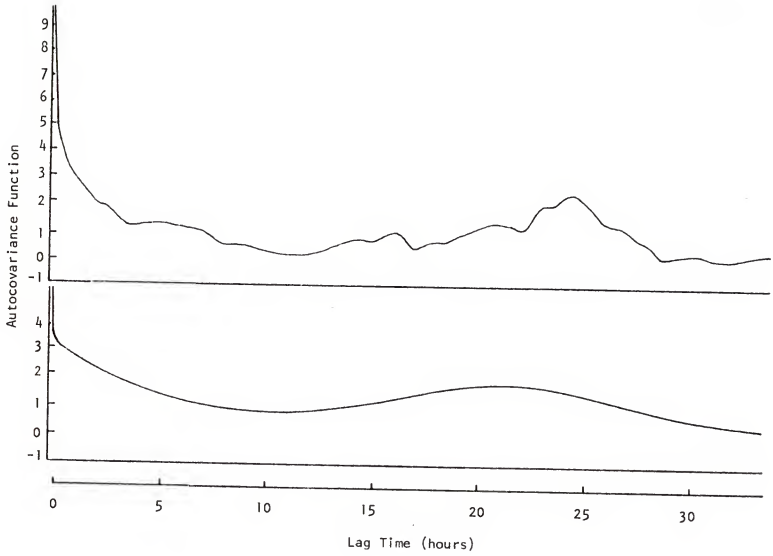

16
8
0
-8
a
b
2
0
-2
c
8
0
-8
d
e
f
Deviation from Mean
0800
2000
0800
2000
Time of Day

Figure 13. Graphs of the autocovariance functions of two swimming activity records of hatchlings from Tortuguero, Costa Rica, plotted against time. LD+t13:11(270:0.1)


Autocovariance Function
9
8
7
6
5
4
3
2
1
0
-1
4
3
2
1
0
-1
0
5
10
15
20
25
30
Lag Time (hours)

activity. This suggests that the bimodal peaks drifted slightly over time.

Crosscovariance analysis (Fig. 14) also gave evidence of higher levels of swimming activity during the photophase and confirmed that the timing of bimodally distributed activity peaks was an individual characteristic. Under the LD+t photoperiod, the turtles were essentially in phase with one another (ψ range was zero to 1.20 hours).

All spectral analyses weakly defined the 24-hour activity period as 22.2 hours (Fig. 15) because the frequency values provided in the computer plot of spectral density function against period allowed no more precise definition in this period range. They were much more precise in the definition of periods shorter than 20 hours. All 24-hour peaks were insignificant at the 80% confidence level, but this does not mean that the turtles did not undergo daily fluctuations in activity levels. They obviously did, as is evident from the moving mean plots. The insignificance probably reflects the facts that the onset and offset of activity were somewhat irregular, and that the daily activity cycle was somewhat blurred by the presence of tidal effects. Also, the time intervals used were appropriate for isolation of infradian rhythms and were not ideal for isolation of a weak period as long as 24 hours from a relatively short activity record.

Omission of a twilight stage from the photoperiod resulted in the loss of an obvious bimodal activity distribution from the activity records of the turtles from Tortuguero (Figs. 16, 17). It also resulted in a delay of the maximum activity levels to the subjective afternoon. Activity indices remained the same as when the photophase included twilight, and no differences from the results of autocovariance, crosscovariance or spectral analyses were found. Neither was there any

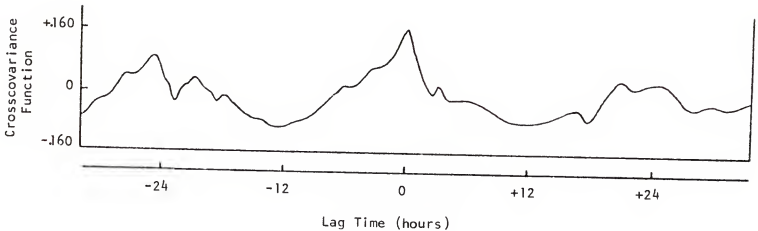


Figure 14. Graph of the crosscovariance function of the swimming activity record of a green turtle hatchling from Tortuguero, Costa Rica, plotted against time. The turtles are 0.172 hours out of phase with each other. LD+t13:11(270:0.1)

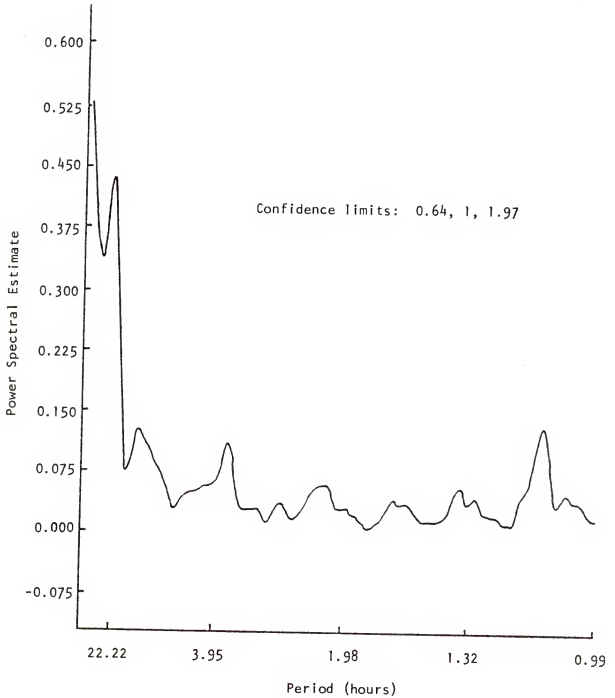
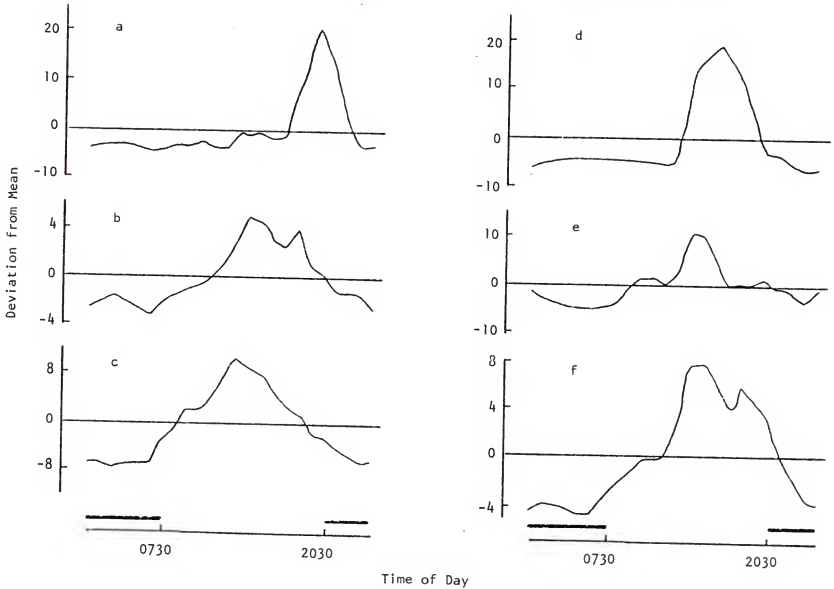


Figure 15. Graph of the power spectral estimates of the swimming activity record of a green turtle hatchling from Tortuguero, Costa Rica, plotted against period. LD+t13:11(270:0.1)

Figure 16. Representative plots of the distribution of swimming activity over time in five green turtles from Tortuguero, Costa Rica. Data were plotted as deviations of three-hour moving means from the daily average activity index. Plot f represents the average of plots a through e.
LD13:11(270:0.1)


a
b
c
d
e
f
20
10
0
-10
4
-4
8
-8
Deviation from Mean
0730
2030
Time of Day

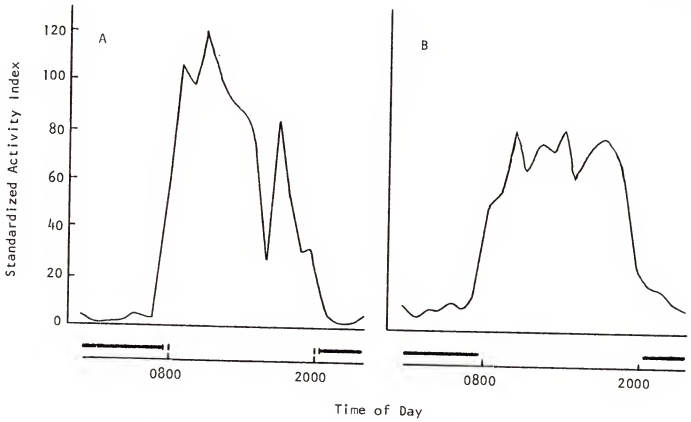


Figure 17. Standardized week swimming activity records of two green turtle hatchlings from Tortuguero, Costa Rica.

A. LD+tl3:11(270:0.1)

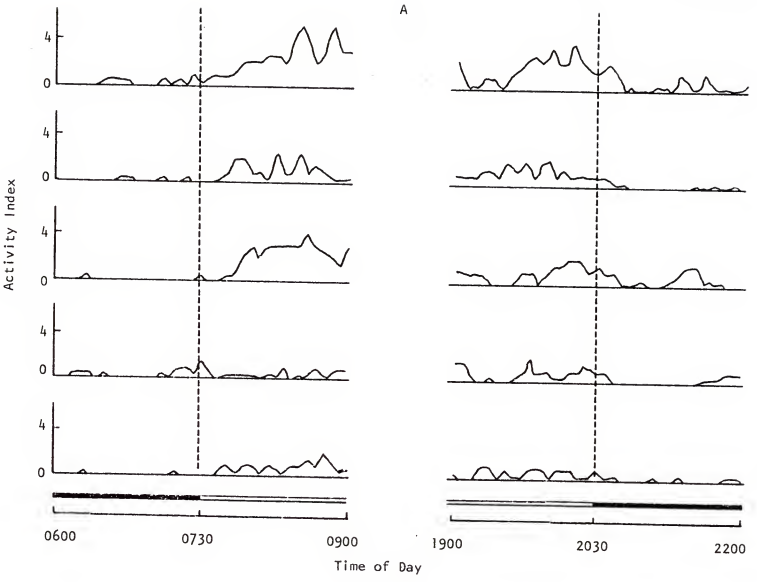
B. LDl3:11(270:0.1)

apparent effect of age on activity patterns. The recorded activity amplitudes were somewhat higher, but this may have been due to the larger size of the older turtles. Visual observation of the turtles verified that small movements of the larger hatchlings activated the event recorder more readily than similar movements of the younger and smaller turtles. In no instance was there a difference in the daily swimming pattern that could be attributed to the change from a 12:12 photofraction to one with a photoperiod of 13 hours.

Since the omission of twilight from the photoperiod resulted in a significant change in the activity pattern of the Tortuguero hatchlings, I considered it necessary to examine in detail the features of activity during the transition between full light and dark in the presence and absence of twilight, and to define the phase relationship (ψ_{onset} and ψ_{offset}) between turtle swimming activity and the photoperiod. Figure 18A shows the standard patterns of activity onset and offset during a photoperiod without a twilight stage. Activity levels characteristically began to increase well after light-on (average ψ_{onset} was -7.6 minutes) and decreased only after the scotophase began. The average ψ_{offset} was -11.8 minutes. The turtles apparently did not anticipate the change in light intensity. When a twilight was interposed between full light and dark, however, the hatchlings (Fig. 18B) began to anticipate the scotophase by decreasing their activity an average of 15.16 minutes before full dark, although they still lagged far behind the start of the photophase (ψ_{onset} averaged -20.80 minutes).

With no dawn or dusk in the photophase, the time of onset of activity of an individual was highly irregular, with an average variation

Figure 18. Graphs of five days of the swimming activity record of one turtle from Tortuguero, Costa Rica, showing the details of activity onset and offset under photoperiods without (A) and with (B) twilight.
LD±t13:11(270:0.1)


A
Activity Index
4
0
0600
0730
0900
1900
2030
2200
Time of Day

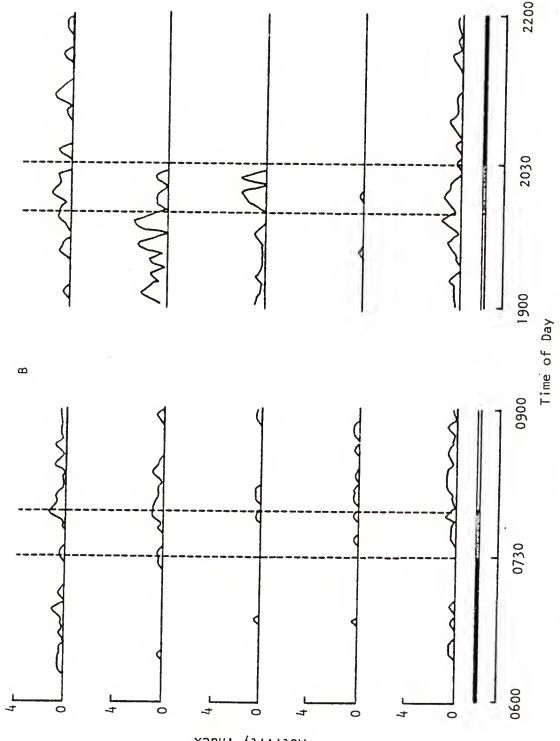


Figure 18. continued.

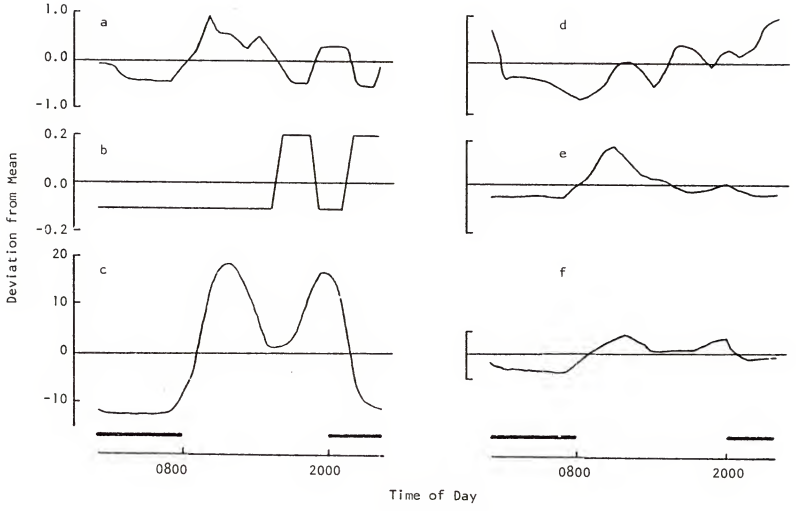
of 36 minutes (range five to 85 minutes) in activity onset times from one day to the next. The ending time of their swimming activity was more constant, averaging only 13 minutes day-to-day variation, with a range of 5 to 25 minutes. Imposition of dawn and dusk reversed the trend, and the cessation time of activity increased in irregularity, averaging 49 minutes with a range of 25 to 80 minutes, in relation to the activity onset time (average variability was 18 minutes with a range of 15 to 20 minutes).

Ascension Island hatchlings

Turtles from Ascension Island showed a bimodal distribution of swimming activity both with and without twilight stages in the photoperiod to which they were exposed (Figs. 19, 20). Like the hatchlings from Tortuguero, their activity indices remained the same from one experimental situation to the other. The average phase angles between the Ascension Island hatchlings, tested in pairs, were similar to those resulting from crosscovariance analyses of the activity records of turtles from Tortuguero. Unlike the Tortuguero hatchlings, they possessed strong infradian and ultradian components of the 24-hour swimming activity cycle (Figs. 21, 22).

The turtles from Ascension Island tended to be more diversified in their activity distribution over time than the Tortuguero hatchlings. Their phase relationship with light-on averaged -8.4 minutes and was almost equal to that of Tortuguero turtles maintained under a photoperiod including twilight. The phase relationship did not, however, change significantly when twilight was removed. At light-off, in all

Figure 19. Representative plots of the distribution of swimming activity over time in five green turtle hatchlings from Ascension Island. Data were plotted as deviations of three-hour moving means from the daily average activity index. Plot f depicts the average of plots a through e. LD12:12(270:0.1)


a
b
c
d
e
f
1.0
0.0
-1.0
0.2
0.0
-0.2
20
10
0
-10
0800
2000
0800
2000
Deviation from Mean
Time of Day

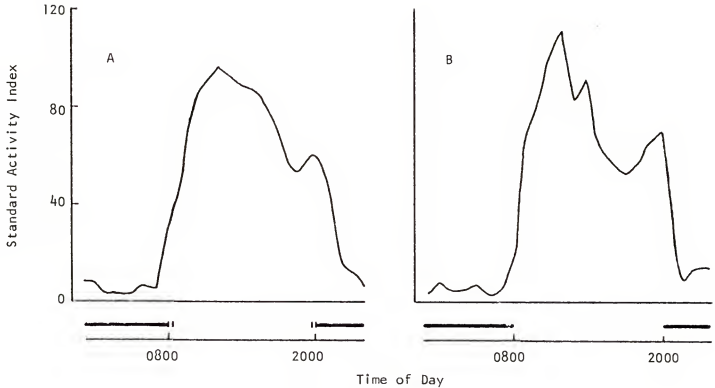


Figure 20. Standardized week swimming activity records of two green turtle hatchlings from Ascension Island.

A. LD+t12:12(270:0.1)
B. LD12:12(270:0.1)

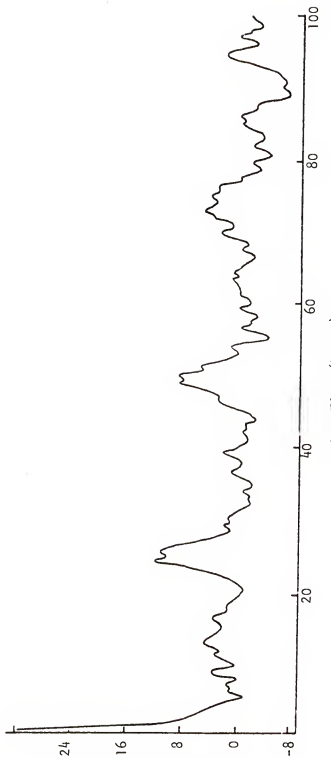


Figure 21. Graph of the autocovariance function of the swimming activity record of a hatchling green turtle from Ascension Island. LD12:12(270:0.1)

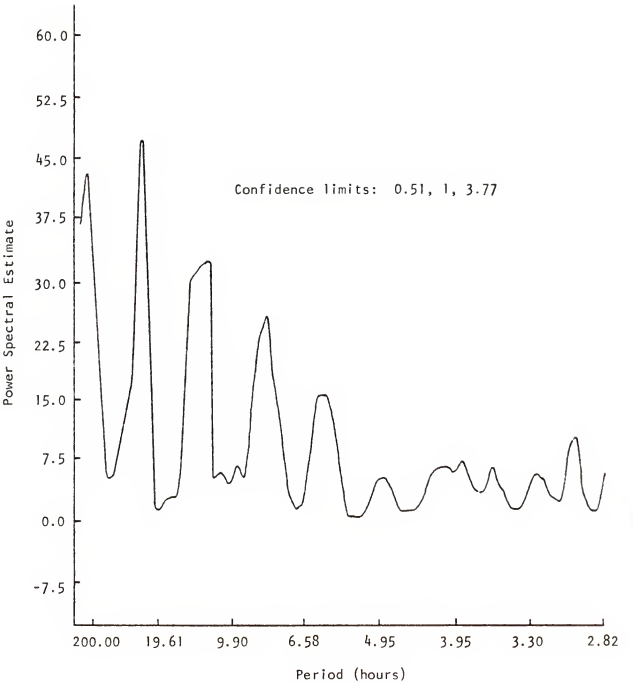


Figure 22. Graph of the power spectral estimates of the swimming activity record of a green turtle hatchling from Ascension Island, plotted against period. LD12:12(270:0.1)

cases, they tended to decrease swimming activity later than the turtles from Costa Rica, showing no indication that they could anticipate the scotophase. The average ψ_{offset} with and without twilight was -18.70 minutes. They were, however, more consistent in maintaining a particular phase relationship with the L-D transition than were the Tortuguero turtles. This is reflected by the greater power of the 24-hour peaks on the spectral density plots. All were significant at the 80% confidence level. The hatchlings from Ascension Island showed no greater degree of diurnalism than did the Tortuguero green turtles.

Galapagos Islands hatchlings

The turtles from the Galapagos Islands were tested only under a LD regimen that included twilight. Hatchlings of carapace lengths and weight equivalent to those of the green turtles tested showed both bimodal (Fig. 23A, 4 turtles) and unimodal (Fig. 23B, 1 turtle) distributions of swimming activity over time. Activity levels were similar to those of all other turtles of equivalent size, and time series analysis of their activity records yielded similar results.

The Free-Running Period and the Effect of Photofraction

All organisms exhibit certain cyclic fluctuations in their physiological and behavioral processes, and most students of these rhythms now agree that those cyclic events with a free-running period (FRP, designated by τ) of approximately 24 hours (termed circadian by Halberg in 1959) have as their basis an endogenous oscillating system (Bünning 1973). The extent to which these rhythms depend on

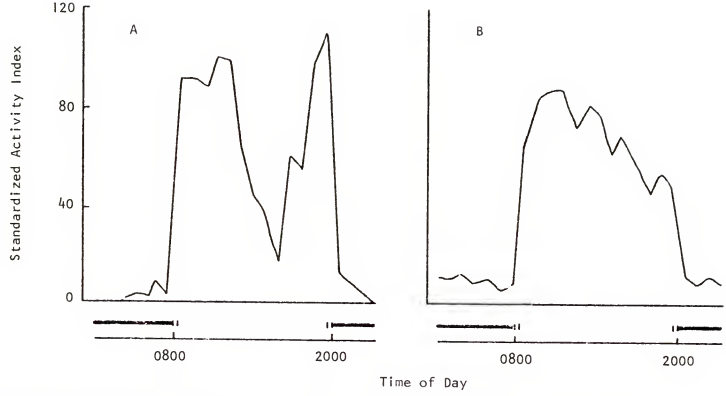


Figure 23. Standardized week swimming activity records of two Pacific black turtle hatchlings from the Galapagos Islands.

A. LD+t12:12(270:0.1)
B. LD+t12:12(270:0.1)

internal and exogenous cues for their timing is, however, still subject to debate (Palmer 1970). Whichever is the case, there can be little doubt that appropriate timing of activities by an organism confers an advantage upon it and is subject to the laws of natural selection.

Circadian rhythms are normally synchronized, or coupled, with each other and with environmental cycles which serve as cues (Zeitgebers). These time the endogenous oscillations and maintain synchronization among them. The daily cycle of illumination is the major time-giver, thought to be capable of entraining all circadian rhythms, although recent work has shown the importance of such Zeitgebers as cyclic variations of temperature, sound, humidity and social cues (Bünning 1973).

The process of entrainment results in control of both the frequency (f) and phase of the circadian cycle (Bünning 1973). The endogenous period is entrained to match the period length of the Zeitgeber (T) in a specific phase relationship (or phase angle, ψ), measured in degrees or units of time, which is characteristic of the species and the stage of life of the individual (Aschoff 1960).

The phase angle denotes the distance between a particular point in the biological cycle and the corresponding point in the exogenous cycle. In rhythm research, the reference point chosen can be, for example, the beginning of activity, which is compared with the dark-light (sunrise) or light-dark (sunset) transition. The phase angle is positive when the biological cycle leads the environmental one and is negative when it lags behind. A phase angle of zero implies that the two cycles are perfectly in phase. Aschoff (1965) suggests that

measurement of the phase angle at the mid-point of the active time is of greater usefulness in determining the phase relationship of the endogenous cycle with the environmental one, but this point may be difficult to determine (Dann 1976, Kenagy 1976) from variable data records.

The endogenous free-running period shown by mammals and birds maintained under constant light (LL) or dark (DD) conditions may extend for as many as 300 cycles before damping out (Eskin 1971, Hoffmann 1971). The constant periods and activity distributions exhibited are known as steady-state values. These may differ among the members of a species (Aschoff 1963, 1965) but are generally consistent in an individual.

In nocturnal homeotherms, the only group studied in detail, the period value appears to be a direct function of the duration of the previous light or dark phase (Pittendrigh and Dann 1976). Endogenous τ values that are influenced by the immediate photoperiodic entrainment history of the animal are called after-effects. These may last up to twenty cycles after the imposition of constant photoperiodic conditions. Any increase (phase-delay) or decrease (phase-advance) in the free-running period that occurs during the transition from one entrained state to another steady-state is defined as a transient.

Although the circadian rhythm of activity represents a persistent property of the endogenous oscillatory system, expression of the activity pattern and its free-running period can be influenced by exogenous non-entraining stimuli. These may directly suppress or attenuate some parts of the pattern, or alter the free-running period. Continuous light and dark, for example, exert different effects on the free-running period and the subsequent fade-out of the circadian rhythm.

The free-running period also varies with light intensity of LL according to Aschoff's rule (Pittendrigh 1960): the free-running period of diurnal animals should decrease with increasing light intensity. The spontaneous frequency ($1/\tau$), the ratio of active time to rest time (α/ρ) and the total amount of activity should increase with increasing light intensity in diurnal animals, according to the circadian rule (Aschoff 1960).

Bünning (1973) summarizes the accepted criteria for the identification of an endogenous circadian rhythm: the rhythm must persist for a substantial number of cycles after the imposition of constant conditions (here constant light and temperature) with a free-running period approximating but not equal to 24 hours. The suspected Zeitgeber (in this case the 24-hour light-dark cycle) entrains the period to exactly 24 hours and sets the phase of the endogenous rhythm.

Procedure

The experiments performed are outlined in Table 5. Data, as in the previous section, were plotted for visual examination and subjected to covariance and spectral analysis. Regression analysis (Sokal and Rohlf 1969) was used to define the free-running period precisely. No standardized weekly averages were calculated because the free-running period is rarely exactly 24 hours and the advance or lag of the rhythm through seven days would render such a plot useless.

The active times had no clear beginning or end in most cases, and it was frequently necessary to identify activity onset and offset by indirect means. The raw data were scanned for occurrence of the

greatest apparent rates of change of swimming activity during each 24 hour period, and the start of the greatest rate of increase was defined as the onset of activity. The end of the greatest rate of decrease therefore represented the activity offset.

Results: the free-running period

Figure 24A and B shows characteristic swimming activity records of young green turtles exposed to continuous light. Hatchlings from Tortuguero older than one week which had been exposed to LD13:11 (270:0.1) and abruptly placed in LL(270) conditions showed temporal patterns of swimming activity as depicted by Fig. 25 after three weeks in the constant light environment. Their records in such conditions were indistinguishable from those obtained when twilight had been part of the previous photoperiodic history of the turtles (Fig. 26). All the Tortuguero hatchlings studied under constant light maintained some degree of circadian activity for at least five cycles, although this was often not readily apparent from visual examination of the raw data. The diurnal activity levels were apparently depressed somewhat after the first day in LL. The α/ρ ratio average was 0.85 under LL, and was 0.78 under all LD conditions. This indicates that the relative durations of swimming and resting (floating) remained unchanged in constant light.

Autocovariance analysis often gave no indication of any circadian rhythm (Fig. 27). Spectral analysis of the same turtles' activity records (Fig. 28) showed significant cycles approximating circadian periodicities together with ultradian and infradian periodicities. In

Figure 24. Swimming activity records of two green turtles from Tortuguero, Costa Rica, exposed to LD12:12(270:0.1), followed by LL(270) and then LD12:12(270:0.1).

A
15 DAYS
ACTIVITY INDEX
TIME

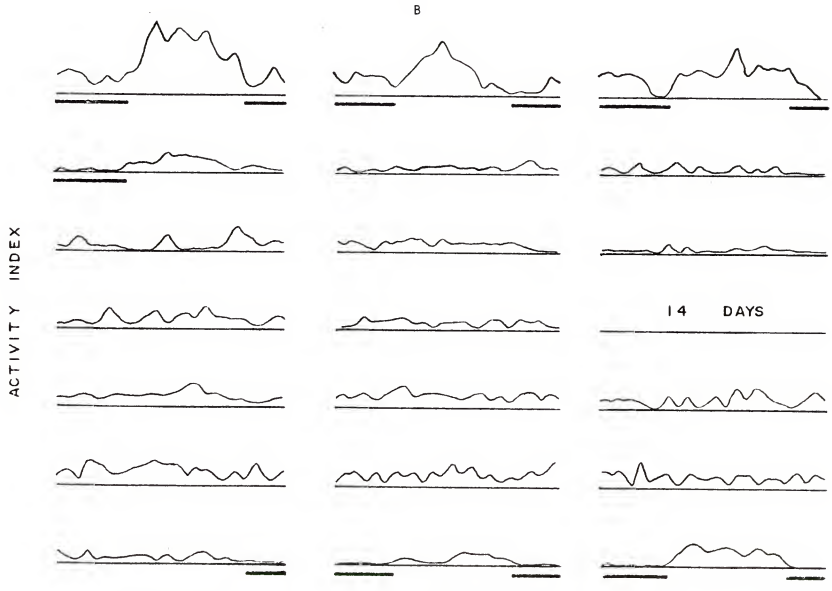


Figure 24. continued.

Figure 25. Representative plots of the distribution of swimming activity over time in five green turtles from Tortuguero, Costa Rica. Data were plotted as deviations of three-hour moving means from the daily average activity index. Plot f represents the average of plots a through e. The turtles were maintained under constant light, and their previous photoperiodic history did not include exposure to twilight.

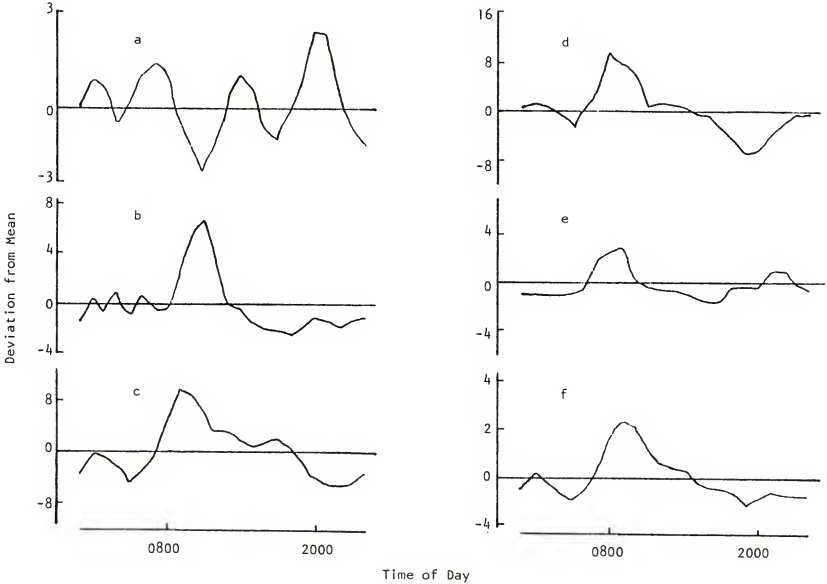
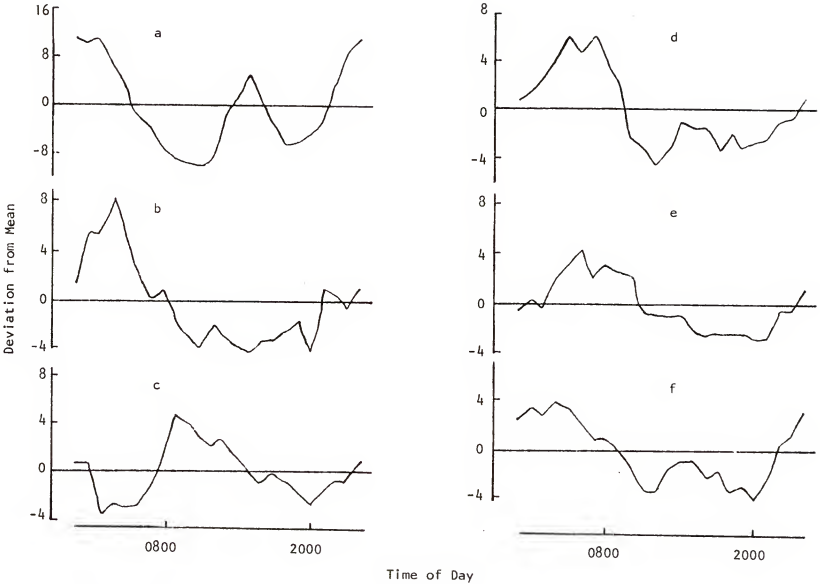

a
b
c
d
e
f
3
0
-3
8
4
0
-4
8
0
-8
16
8
0
-8
4
0
-4
4
2
0
-4
0800
2000
0800
2000
Deviation from Mean
Time of Day

Figure 26. Representative plots of the distribution of swimming activity over time of five green turtles from Tortuguero, Costa Rica. Data were plotted as deviations of three-hour moving means from the daily average activity index. Plot f represents the average of plots a through e. The turtles were maintained under constant light, and their previous photoperiodic history included exposure to twilight.


a
b
c
d
e
f
16
8
0
-8
4
-4
0800
2000
Deviation from Mean
Time of Day

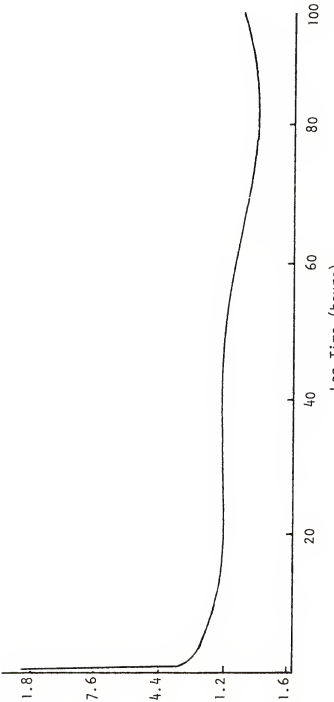


Figure 27. Graph of the autocovariance function of the swimming activity record of a hatchling from Tortuguero, Costa Rica, plotted against time. LL(270)

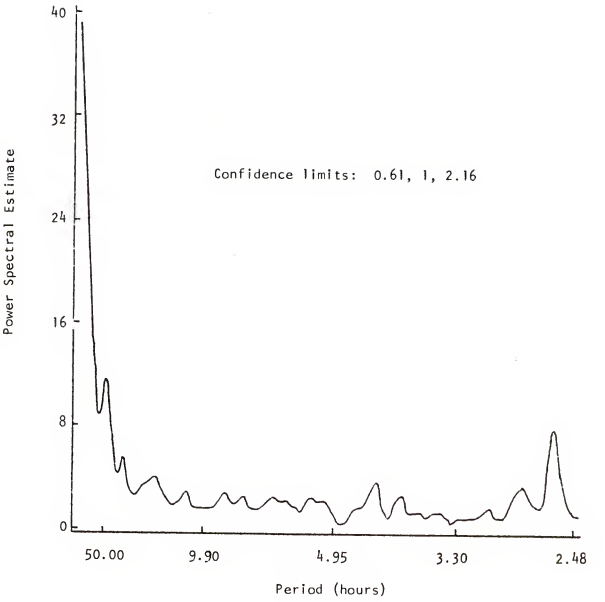


Figure 28. Graph of the power spectral estimates of the swimming activity record of a green turtle hatchling from Tortuguero, Costa Rica, plotted against period.
LL(270).

most instances, however, both autocovariance and power spectral analysis (Figs. 29, 30) gave evidence of cyclic activity. The hatchlings were no longer in phase with each other (Fig. 31). They now exhibited a phase angle range of from 0.01 to 3.42 hours.

Ascension Island turtles under LL(270) conditions (Fig. 32) showed daily activity patterns identical with those exhibited by turtles from Tortuguero. They had approximately the same α/ρ ratios, with an average of 0.92, as they had under LD conditions (0.85), although the absolute amounts of activity approximately doubled when constant light was imposed. The circadian or other periodicities were minimally reflected in plots of the autocovariance functions against time (Fig. 33), but were readily apparent in plots of the spectral density estimates (Fig. 34). These also isolated ultradian periods of approximately 40 and 200 hours from all the records, and infradian cycles of approximately 11 hours from some. These turtles were much more out of phase with one another (Fig. 35), averaging phase angles of 0.72 to 4.85 hours, than were the Tortuguero hatchlings. No differences in the temporal patterning of swimming activity as a result of the presence or absence of twilight in the photoperiodic history of the turtles were defined.

All turtles for which the free-running period could be calculated by regression analysis (Table 6) exhibited periods of less than 24 hours, but the Tortuguero hatchlings were more precise in their timing than those from Ascension Island.

Regardless of whether twilight was present in the preceding photoperiod, all the turtles took an average of five to seven cycles to attain

Figure 29. Graph of the autocovariance functions of the swimming activity records of two hatchlings from Tortuguero, Costa Rica, plotted against time.
LL(270)

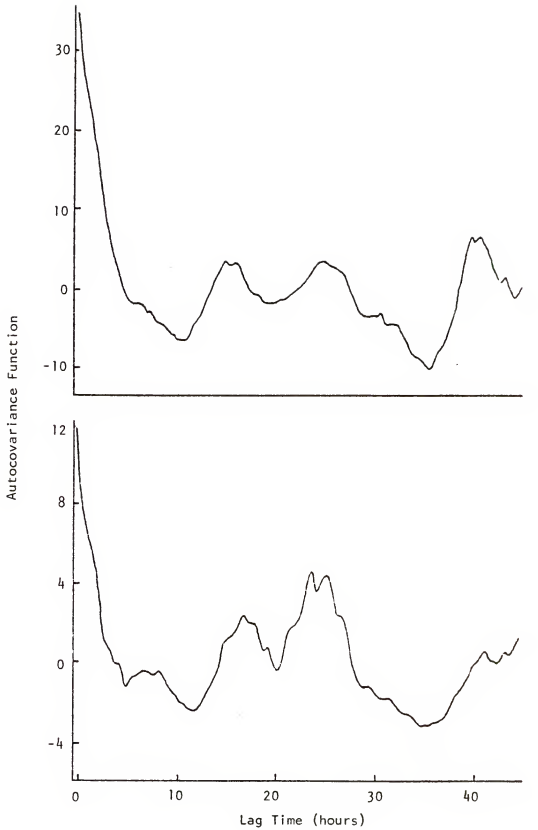
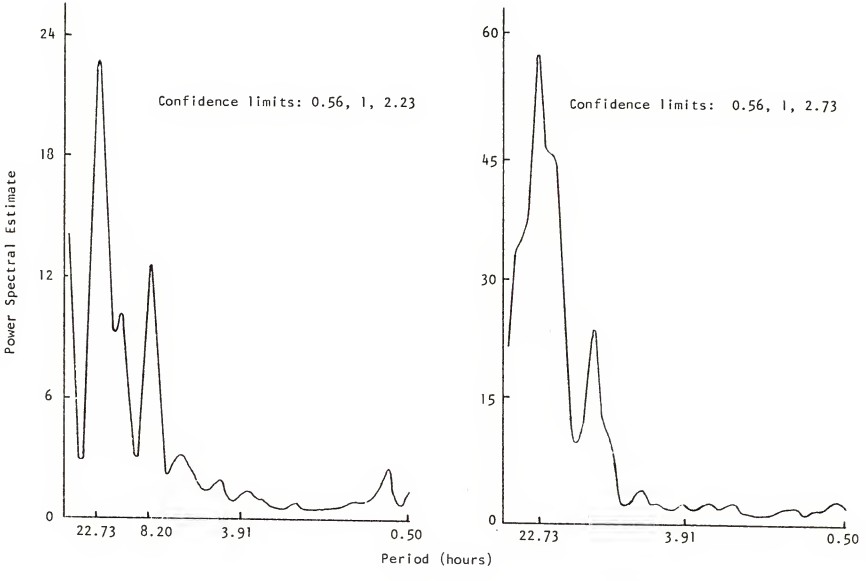

30
20
10
0
-10
12
8
4
0
-4
Autocovariance Function
0
10
20
30
40
Lag Time (hours)

Figure 30. Graph of the power spectral estimates of the swimming activity records of two green turtle hatchlings from Tortuguero, Costa Rica, plotted against period.
LL(270)


Power Spectral Estimate
24
18
12
6
0
Confidence limits: 0.56, 1, 2.23
22.73
8.20
3.91
0.50
60
45
30
15
0
Confidence limits: 0.56, 1, 2.73
22.73
3.91
0.50
Period (hours)

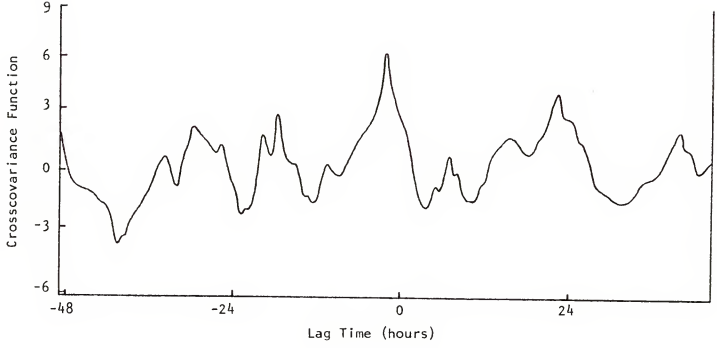
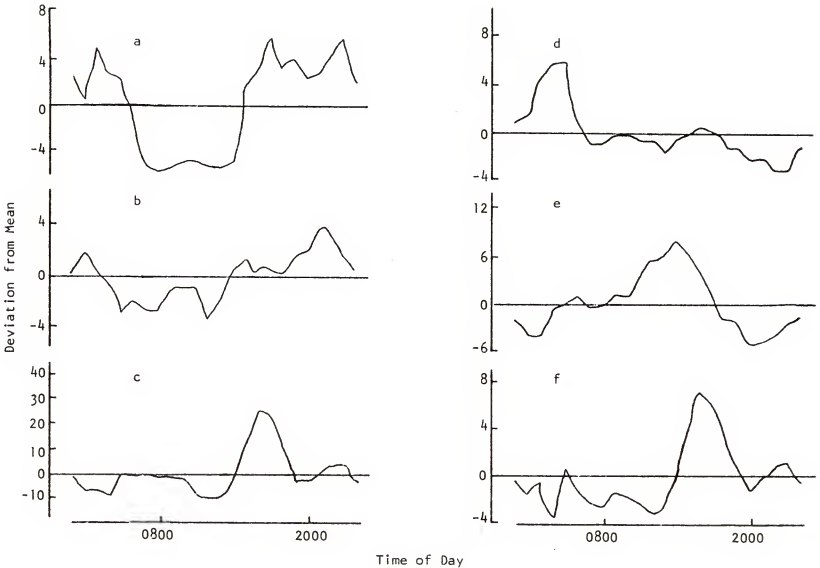


Figure 31. Graph of crosscovariance function of the swimming activity records of two green turtle hatchlings from Tortuguero, Costa Rica, plotted against time. LL(270)

Figure 32. Representative plots of the distribution of swimming activity over time in five green turtles from Ascension Island. Data were plotted as deviations of three-hour moving means from the daily average activity index. Plot f represents the average of plots a through e. The turtles were maintained under constant light, and their previous photoperiodic history included exposure to twilight.


a
b
c
d
e
f
8
4
0
-4
4
0
-4
40
30
20
10
0
-10
8
4
0
-4
12
6
0
-6
8
4
0
-4
0800
2000
0800
2000
Deviation from Mean
Time of Day

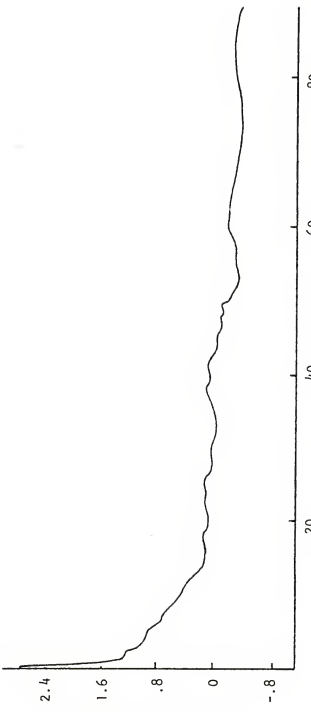


Figure 33. Graph of the autocovariance function of the swimming activity record of a hatchling green turtle from Ascension Island, plotted against time. LL(270)

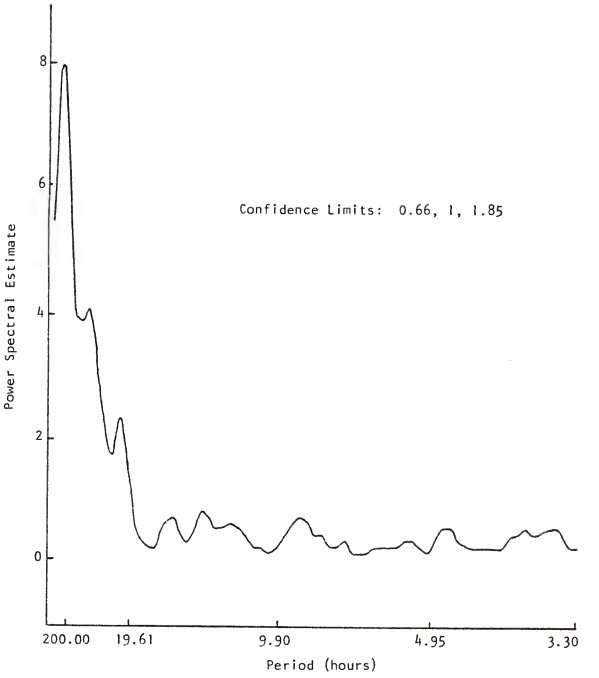


Figure 34. Graph of the power spectral estimates of the swimming activity record of a green turtle from Ascension Island, plotted against period.
LL(270)

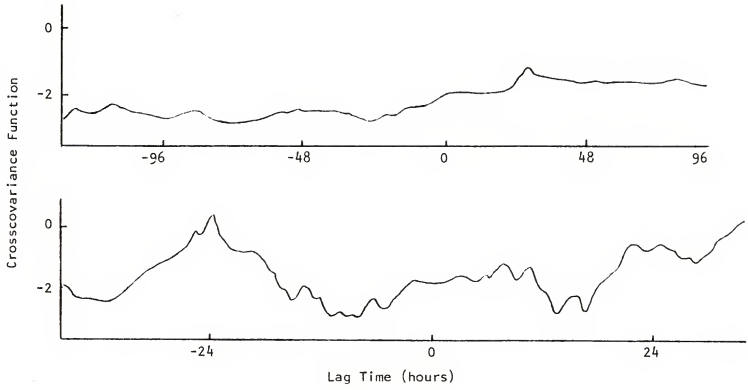


Figure 35. Graphs of the crosscovariance functions of the swimming activity records of four green turtles, taken in pairs, from Ascension Island, plotted against time. LL(270)

Table 6. The free-running periods of green turtle hatchlings from Tortuguero, Costa Rica, and Ascension Island maintained under constant light after exposure to photoperiods with and without twilight.

Source of Turtles	Previous Photoperiodic History LD	+ twilight	- twilight
Tortuguero	12:12	22:56.57±9.56	22:25.09±7.26
		23:48.56±2.32	23:48.11±6.39
		22:32.16±7.47	22:42.49±4.07
		22:07.48±6.38	22:10.37±9.16
		22:46.10±5.56	
		23:39.02±3.04	
		22:11.32±6.43	
	13:11	22:53.44±6.22	22:26.12±9.11
		22:42.04±3.67	22:23.25±4.04
		22:36.17±3.29	22:17.48±7.41
		22:21.26±5.46	
Ascension Island	12:12	22:21.00±17.59	23:59.04±13.76
		22:46.43±17.42	22:46.51±16.43
		23:15.43±32.07	22:27.21±21.27
		22:54.37±19.57	

FRP given in hours:minutes.seconds±minutes.seconds.

a new steady state free-running period in constant light. Examination of the event recorder records of swimming activity showed that the turtles characteristically began their first "day" in constant light with a large advancing (shorter period) transient, followed by advancing transients with phase angles of progressively decreasing magnitude until the new steady-state free-running period was attained. In a few cases (four Tortuguero hatchlings and two from Ascension Island) the advancing phase transients alternated with delaying (longer period) ones of progressively smaller magnitude until the free-running period reached a new steady state value.

Results: effect of phase shift and photofraction

It was not possible to subject the hatchlings to the 90° phase shifts which are the standard test of photoperiod as a Zeitgeber because of the need to leave the experimental room suitable for others' work, so the hatchlings were subjected to three hour (45°) phase shifts instead. They were also subjected to progressively increasing photofractions, to further examine the entraining effect of photoperiod on the activity cycle.

Tortuguero green turtle hatchlings subjected to progressively increasing photofractions in a 24-hour day exhibited fairly stable activity patterns over time (Fig. 36). Their major swimming activity occurred during the "afternoon," beginning at about 1500 LST regardless of the length of the photophase. The activity peak widened (Fig. 36 a through c) as photofractions increased from 12 to 16 hours, but beyond 16-hour photofractions the "afternoon" burst of swimming lasted no

Figure 36. Standardized week swimming activity records of a green turtle hatchling from Tortuguero, Costa Rica, exposed to increasing photofractions in a 24-hour day which included twilight in the photophase.

a) LD+t12:12
b) LD+t14:10
c) LD+t16:8
d) LD+t18:6
e) LD+t20:4
f) LD+t22:2
100
50
0
0800
2000
Standardized Activity Index
Time of Day

longer than it had under the LD+t12:12 photoperiod, ending at approximately 1900 LST. The "morning" activity bout involved less overall activity than the "afternoon" one, and was maintained at a relatively stable phase angle to dawn onset until the photofraction increased beyond 18 hours. It then returned to the same time period it had occupied under the LD+t12:12 photoperiod. Both major swimming bouts continued to occur at the same respective times after the turtles were exposed to LL and then returned through LD+t18:6 to LD+t12:12. All the turtles experienced a gradual decline in absolute amounts of swimming activity (Table 7) as the photoperiod approached LL conditions. The equality between the photofraction and the number of hours of active swimming (α) broke down as soon as the day contained more than 14 hours of light. The turtles reduced the relative number of hours they devoted to activity. The degree of diurnalism (d/n, or the concentration of major activity in the photophase) also declined as photofraction increased, as did the absolute difference (s/r) between "swimming" and "resting" levels of activity. In other words, activity tended to be more evenly distributed over the 24-hour day, and even the so-called "rest" times included some swimming. Figure 37 demonstrates the relatively constant distribution over time of swimming activity bouts through increasing photofractions. The greatest variability in amounts of swimming came late in the day for most of the turtles, as delaying dusk affected activity offset. A similar degree of variability was evident in the early morning hours.

All turtles fully adjusted to advancing or delaying photoperiods within three to five days (Fig. 38). Their adjustment speed and accuracy

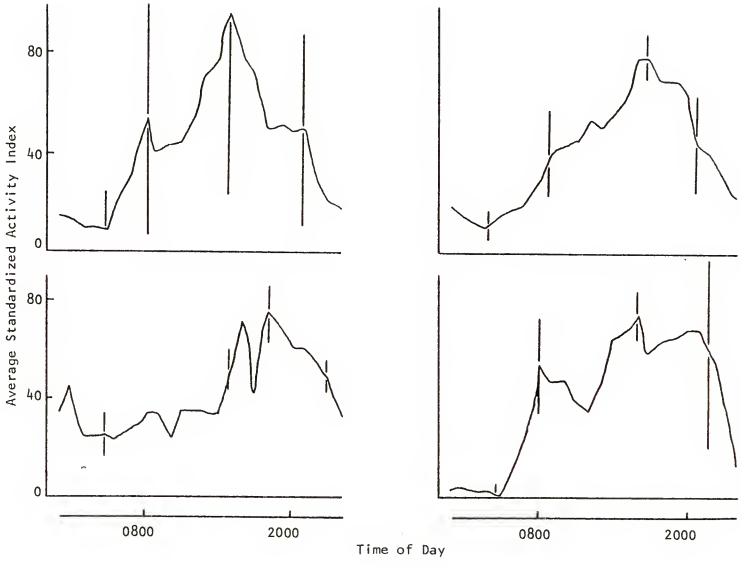
Table 7. Summary of the features of swimming activity distribution of five green turtle hatchlings from Tortuguero, Costa Rica, exposed to increasing photofractions.

Turtle	LD+t(270:0.1) 12:12	14:10	16:8	18:6	20:4	22:2
1	9.88±8.72 1 1 6.37 6.37	8.71±9.55 1.4 1.4 5.50 5.50	15.29±11.97 2 1.18 4.61 3.40	4.90±7.78 3 0.85 4.48 3.73	2.89±3.46 5 1.4 5.34 4.21	3.84±2.66 11 0.85 5.07 4.25
2	8.03±9.34 1 1 9.58 9.58	6.99±8.64 1.4 1.4 8.85 8.85	6.76± 6.30 2 1 12.44 4.27	9.17±7.64 3 0.85 9.67 3.10	4.82±5.07 5 1.4 9.82 3.56	3.98±3.76 11 0.71 9.34 3.40
3	3.48±4.25 1 1 7.29 7.29	1.74±1.82 1.4 1.4 5.31 5.31	1.80± 1.83 2 0.85 2.66 2.43	4.89±5.55 3 0.85 2.66 2.39	1.43±1.57 5 1.4 3.03 2.91	1.27±1.22 11 0.85 2.86 2.83
4	8.31±8.20 1 1 8.91 8.91	5.09±6.00 1.4 1.4 6.79 6.79	5.75± 5.92 2 0.85 14.08 4.75	8.75±7.89 3 0.85 2.10 2.22	4.08±4.65 5 1.4 2.34 2.34	4.35±3.49 11 0.85 1.57 2.25
5	5.58±4.67 1 1 6.25 6.25	2.47±2.53 1.4 1.4 4.83 4.83	2.39± 3.37 2 0.60 1.36 2.63	3.30±3.35 3 0.60 1.33 1.91	2.08±2.30 5 0.71 1.69 2.15	1.79±2.55 11 0.60 1.46 3.39

Average Activity Index
L/D α/ρ
d/n s/r

Figure 37. Graph showing the average hourly standardized activity indices of four turtles from Tortuguero, Costa Rica, exposed to photofractions ranging from 12 to 22 hours, and which included twilight.

| standard deviation


Average Standardized Activity Index
80
40
0
80
40
0
0800
2000
0800
2000
Time of Day

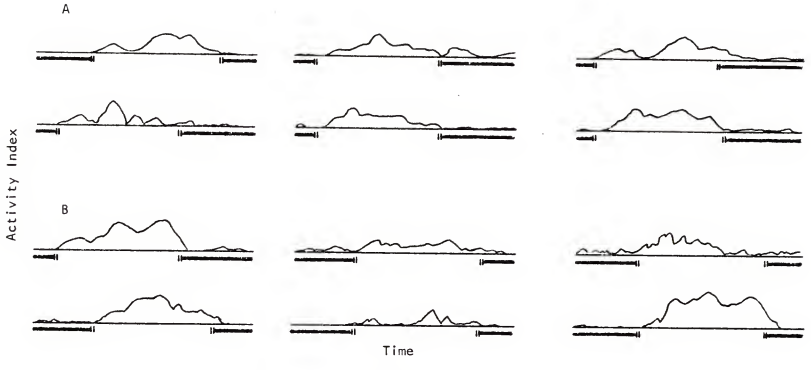


Figure 38. Graphs of the swimming activity records of a green turtle hatchling from Tortuguero, Costa Rica, exposed to a three-hour phase advance (A) and a three-hour phase delay (B) of the photoperiod.
LD+t12:12(270:0.1)

did not apparently depend on the presence or absence of twilight in the photophase. They characteristically regained a constant activity-onset phase angle with the advanced photoperiod within one cycle, and more slowly adjusted the activity-offset angle. When the photofraction onset was delayed (Fig. 38B), the turtles again quickly adjusted (within two days) their activity-onset time to maintain a negative phase angle of approximately 20 minutes, and took about four cycles to regain the phase angle characteristic of activity-offset.

Tidal Rhythms

The periods of many behavioral rhythms are known to correlate closely with cycles in the environment; one example is the correlation of rhythms of locomotor activity with tidal (lunar-day) cycles. Many marine animals (see reviews by Fingerman 1960, Schwassmann 1971a) time such activities as emergences, vertical migrations and breeding to tide levels, and even animals far removed from the marine environment have been reported to show tidal rhythms (Brown and Terracini 1959, Brett 1971) with the suggestion of endogenous components.

The tidal rhythm of locomotor activity may be difficult to identify visually in an activity record due to its interaction with or masking by the circadian activity rhythm (Webb and Brown 1959, Bünning 1973). Mathematical analysis of the record can reveal both periodicities. They may react differently to the imposition of continuous light, and it has been hypothesized that each periodicity is under the control of one or more separate clocks, with the tidal rhythm synchronized by other than photoperiodic cues. The tidal rhythm itself may reflect

one oscillator with a period of 12.4 hours, or two superimposed oscillators with 24.8-hour periods.

The hatchling sea turtle, if pelagic, would have little direct exposure to the effects of tides, but the possibility of the existence of a tidal rhythm in these marine reptiles required investigation.

Methods and Results

Activity records of green turtle young from Tortuguero, Costa Rica, and from Ascension Island were visually examined for the presence of solar and tidal rhythms, but it was impossible to define anything other than an apparent solar period in the plotted data. An analytical method reported by Brett (1971), essentially a form of autocorrelation analysis (Jenkins and Watts 1968), was therefore adapted for use in rhythm isolation.

The average tidal delay rate is 51 minutes per day, and if one assumes two tidal changes per day, then averaging the hourly activity indices of 24 days of a hatchling's swimming activity would allow movement of the tidal effects through a full 24 hours, and would effectively damp out any reflection of them on a plot of the averaged data. Any solar effect would, however, still be apparent, provided, as is the case with these hatchlings, that the free-running period approximates 24 hours.

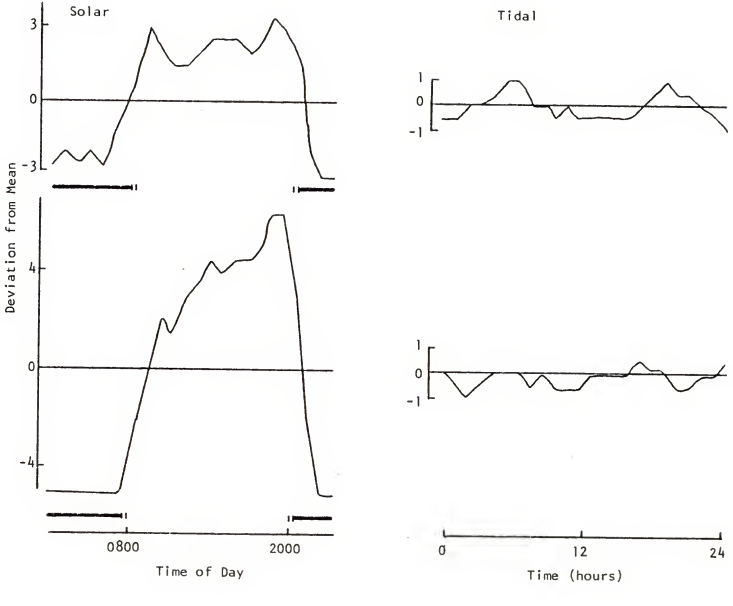
A similar averaging process designed to damp out the solar portion of the swimming rhythm would show whether or not a tidal activity rhythm was present. This analysis required alignment of the lunar days, so that the hourly activity indices were advanced one hour per solar

day for each of five consecutive days. The sixth day was not advanced, and the process was repeated to provide a total of 28 lunar days of data for averaging. This achieved an advancement of 300 minutes over six solar days; advance roughly equivalent to the tidal rate of 306 minutes (Brett 1971). It was sufficient to maintain an alignment of the tidal effects. The use of 28 days of data allowed the solar effect to move through 24 hours, and thus be extinguished in the averaging process.

The resultant average activity values were then plotted as the deviation of the three-hour moving means from the daily average. This permitted easy visual identification of whatever rhythmic activity was depicted by the plot.

The analyses were first performed on data collected from five hatchlings from Tortuguero and five from Ascension Island maintained under an LD cycle with and without twilight. Figure 39 reflects the definite solar rhythm present in the swimming activity of the turtles from Costa Rica, and a weaker but distinct tidal component. The absence of twilight, in all cases, resulted in a slight reduction of the amplitude of activity attributable to the tidal cycle. In all cases, the activity levels of the active (α) hours were significantly greater ($p < 0.01$) than those of the rest (ρ) hours. The activity amplitude of the most active hour was greater ($p < 0.01$) than that of the least active hour in the solar component of the swimming rhythm, but these levels were equal in the lunar component of each hatchling's activity. No apparent difference between the Tortuguero and Ascension Island turtles was revealed in these results.

Figure 39. The solar and tidal components of the daily swimming activity records of two turtles from Tortuguero, Costa Rica, maintained under LD+t13:11(270:0.1).


Solar
Tidal
Deviation from Mean
3
0
-3
4
0
-4
1
0
-1
1
0
-1
0800
2000
Time of Day
0
12
24
Time (hours)

Analysis of data collected from turtles maintained under continuous light gave evidence that both the tidal and solar components of swimming activity rhythms were subject to endogenous control (Fig. 40). Activity amplitudes in the active hours were in all cases significantly greater ($p < 0.01$) than those in the inactive hours. The difference between the maximum and minimum hourly activity levels was, however, significant in both the solar ($p < 0.01$) and tidal ($p < 0.05$) components of the swimming rhythm in approximately half of the hatchlings tested from each region. There was no apparent effect of the presence or absence of twilight on the subsequent activity under constant light.

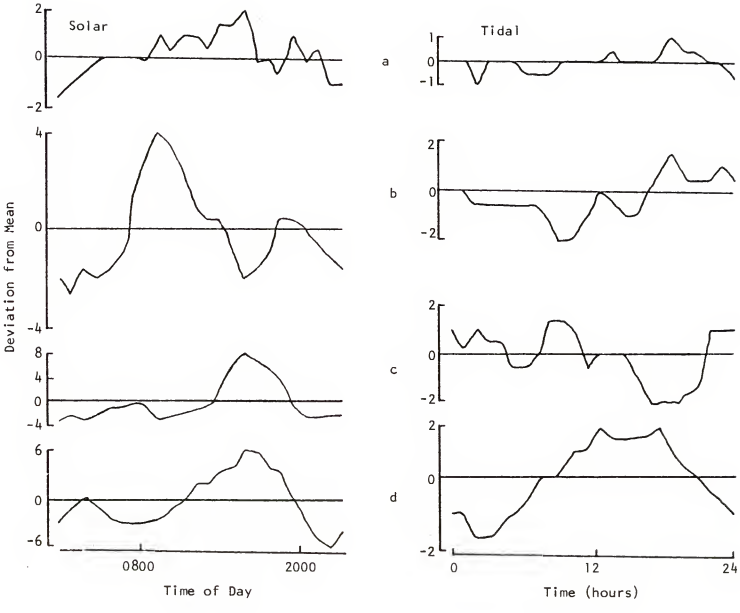
It is, of course, possible that the hatchlings were still able to time their activity by some environmental cue not apparent to the experimenter during their time in constant light and temperature. There are no reports on the sensitivity of sea turtles to fluctuations in such subtle potential cues as the geomagnetic or electrical field and therefore there is at present no way to predict the possible effect of their elimination on turtle behavior.

There was no evidence of a lunar (monthly) rhythm in any of the data collected.

Summary of Results

1. Green turtle hatchlings from Tortuguero, Costa Rica, exhibited a bimodal distribution of swimming activity over time, with activity concentrated in the photophase, when twilight was present in the photoperiod. Activity was unimodally distributed when twilight was absent. All turtles were roughly in phase with one another. The activity pattern was not a function of age.

Figure 40. The solar and tidal components of the daily swimming activity records of two turtles from Tortuguero, Costa Rica (a, b), and two from Ascension Island (c, d) maintained under LL(270).


Solar
Tidal
Deviation from Mean
a
b
c
d
2
0
-2
4
0
-4
8
4
0
-4
6
0
-6
1
0
-1
2
0
-2
2
0
-2
2
0
-2
0800
2000
0
12
24
Time of Day
Time (hours)

2. In the absence of twilight, activity-onset lagged behind light-on by an average of seven minutes. Offset lagged behind light-off by 11 minutes. When twilight was added to the photoperiod, the phase angle of activity onset was -20 minutes, and that of activity offset was +15 minutes. Without twilight, activity-onset was more irregular in time than offset, but the situation was reversed with the imposition of twilight.
3. Hatchlings from Ascension Island showed a bimodal activity distribution with and without twilight as part of the photophase. There were strong infradian and ultradian components of the distribution of swimming activity.
4. With or without twilight, the average phase angle of activity-offset was -18.70 minutes, and the onset angle averaged -8 minutes. The Ascension Island turtles were much more precise in their timing than the hatchlings from Tortuguero.
5. Steady-state free-running periods were defined in 72% of the hatchlings from Tortuguero and in 70% of those from Ascension Island, and the presence of twilight had no effect on the periodicity established. The remaining turtles exhibited a free-running period which damped out after five to seven cycles. All free-running periods were shorter than 24 hours, ranging from 22:07.48 to 23:59.04. There was no difference between the free-running periods established by the two groups of turtles. Most Tortuguero turtles decreased activity levels very slightly in LL, and stayed approximately in phase with one anther, while the activity levels of the Ascension Island hatchlings increased twofold, and the turtles drifted out of their LD phase relationships.

6. All Tortuguero hatchlings adjusted to phase shifting within three to four cycles, but showed some independence from the photoperiod in the phasing of their swimming activity when the photofraction increased beyond 16 hours.
7. All hatchlings, regardless of age, exhibited weak tidal rhythms of swimming activity in both LD and LL.

Discussion

It is thought that hatchlings at the ages of those studied are normally associated with drifting Sargassum rafts. The data obtained in this study might have been a more reliable representation of natural activity if such rafts had been provided for the turtles, but my recording method would not have picked up the activity of turtles on rafts. The lack of rafts may have led to a departure of the activity levels from normal, but it is doubtful that the temporal pattern of swimming would have been affected.

Green turtle hatchlings, regardless of age, are definitely diurnal in their swimming activity, and the photophase activity is bimodally distributed under photoperiods approximating those in their natural environment. They behave in accordance with the standard circadian rhythm pattern suggested by Aschoff in 1966. A question still stands, however, as to whether or not this activity distribution reflects that which one would observe in hatchlings on floating Sargassum rafts in the open ocean. According to the Atlas of the North Atlantic Ocean, Section II (Anon. 1967), the sea surface temperatures in the regions in which the hatchlings might be located approach and

exceed 27°C. At temperatures only slightly greater than this (Bustard 1967, Mrosovsky 1968) the activity of green turtle hatchlings is thermally inhibited. It seems possible, then, that the activity of hatchlings in the ocean might be thermally influenced to become crepuscular, confined to dawn and dusk, instead of being spread over the daylight hours.

All the turtles were definitely responsive to the ambient photoperiod in the timing of their swimming activity, an indication of the effect of the photoperiod on the fundamental biological clock. Studies on the setting of phase relationships of circadian rhythms by homeotherms and plants (Aschoff 1969, Pittendrigh 1974) have defined six factors which might be involved:

1) The natural free-running period of the organism;
2) The physiological and behavioral state of the organism, which might influence its phase-response thresholds;
3) The LD ratio (intensity and/or duration);
4) The intensity of illumination;
5) The duration and spectral characteristics of twilight; and
6) Environmental factors other than the photoperiod.

Dann and Aschoff (1975) suggest that some features of timing are characteristic of all animals. They state, for example, that the beginning of activity is frequently more precise than the activity offset, and that both are more precise if they occur during civil twilight. The green turtles studied here conformed to this rule in that, with twilight in the photophase, the onset of activity was more precise than the offset, although the rule did not hold in the absence of twilight. The differences in the characteristics of the timing of activity-onset and

offset, reflected in the reaction to a photoperiod phase shift, could mean that swimming activity is based on a coupled oscillation model similar to that described by Pittendrigh (1974), and also discussed by Hoffmann (1971) and Gwinner (1974). Pittendrigh suggests that the beginning and end of activity are coupled to two separate oscillator populations which are in turn synchronized to the light-dark transition, one to dawn and the other to dusk, with the phasing of activity-offset set primarily by the photoperiod duration and the total light intensity present at dusk. Both oscillators are then mutually synchronized to form an integrated circadian system.

In continuous light, these separate systems could be expected to split into two free-running rhythms with different periodicities. The overall activity pattern is then determined by the dominant oscillator. One of these free-running rhythms, usually the more precise (Pittendrigh 1974), may drift in relation to the other until the previous LD phase relationship is regained. This would only be apparent during extended studies (100+ days) of activity under constant conditions.

Many animals are exposed to seasonal variations in photofraction. As dawn and dusk move farther apart or closer together in time, phase relationships change and mutual coupling between the oscillators tied to dawn and dusk might either break down or remain strong enough to resist the "pull" of the changing light-dark transition times. Animals characteristically respond to the increase of photofraction with season by starting activity earlier in absolute time but later in relation to the onset of dawn (Dann and Aschoff 1975). They terminate activity later in real time but relatively earlier in relation to sunset. Although

the green turtle hatchlings in a tropical or subtropical natural environment are not usually exposed to drastically changing photofractions, they apparently responded to them in the "usual" fashion. Their overall activity pattern under increasing photofraction remained relatively stable, with the activity beginning and ending farther away in time from the light-dark transition.

Most of the hatchlings exhibited a measureable free-running period of less than 24 hours in the absence of synchronizing cues in keeping with Aschoff's (1960) prediction, although the duration of the period was somewhat variable. The recorded swimming activity of the turtles, as measured here, included several components of activity such as the search for food, exploration and position adjustment. It is possible that these various behaviors have slightly different free-running periods. Under constant light, the overall activity period resulting from the superimposition of these periodicities might therefore appear relatively imprecise and be subject to rapid dissociation and fade-out. This dissociation might have been partially responsible for the slight imprecision in free-running periods exhibited by the green turtle hatchlings as compared to those measured for vertebrates having only one activity criterion, such as wheel running, as the basis of the free-running period. It might also account, in part, for the absence of a distinguishable free-running period in 30% of the experimental animals.

Many environmental factors can influence the nature of the free-running period of an organism. If phasing depends primarily on the twilight portion of the photophase, then the characteristics of that

twilight are extremely important. Bünning (1973) reports that light intensities of approximately 10 lux are the most effective in eliciting a precise phase-response in animals. The twilight to which the turtles were exposed, besides being a step decrease in light, was composed of light of 10 times this intensity. This may have contributed to the lack of precision in the subsequent free-running periods. It should also be noted that the precision of timing of swimming rhythms by the turtles could have been affected by the spectral distribution of the light to which they were exposed. Some LL can cause dampening of a behavioral cycle, and the laboratory lights were deficient in the far red, which is especially effective in phasing plants and some animal cells and organelles. The free-running period might also have been steadier if refuge from constant light had been provided (Harker 1960).

The sea turtle hatchlings did possess a time-sense, but it is doubtful that a biological clock with the accuracy of that demonstrated by the turtles is precise enough to serve as the basis for navigation. It is possible, however, that greater accuracy of the time-sense might be demonstrated by turtles exposed to light intensities or to spectral distributions different from those used in this study.

The readjustment of the turtles' free-running periods to exactly 24 hours upon imposition of an LD cycle is suggestive of entrainment, but does not actually prove it (Bünning 1973). The effectiveness of the LD cycle as a Zeitgeber was confirmed by the three-hour light cycle shift to which the turtles' activity rhythms responded and gradually recovered certain phase angles characteristic for the particular photoperiod.

An oscillator, to be entrainable by an exogenous cyclic variable, must be differentially responsive to it over the duration of its cycle (DeCoursey 1961, Hoffmann 1968). This feature of sea turtle oscillatory systems has yet to be investigated. It can only be suggested, then, that the temporal distribution of green turtle hatchling swimming activity is subject to entrainment by features of the photoperiod, such as its duration, its intensity, and the rates of change of light intensity during twilight (Aschoff 1969). Much research in this area remains to be done.

PATTERN DEVELOPMENT

The preceding sections have described the activity of green turtle and Pacific black turtle hatchlings as they enter the water for the first time and undergo their characteristic swimming frenzy, as well as the activity of older hatchlings as they were exposed to various photoperiods. It is the purpose of this section to provide a brief summary of the transition of swimming activity from the frenzy stage to the stable diurnal temporal distribution shown by older turtles.

Procedure

The data presented here were collected from swimming records of hatchlings whose activity was recorded from the time of their initial entry to water through a minimum of 12 subsequent days (refer to Table 5). Such data were collected for turtles from Tortuguero exposed to light-dark cycles with and without twilight, and for turtles from Ascension Island exposed to LD cycles containing twilight in the photophase. A limited amount of data on the temporal distribution of swimming in Ascension Island and Tortuguero hatchlings under LL was obtained in the swimming frenzy experiments (Table 1) which were continued for 10 to 12 days. This activity was compared to that recorded for other, older hatchlings. All the data were subjected to analytical methods described elsewhere in this paper.

Results and Discussion

Young Tortuguero green turtle hatchlings of both the small and the large size phases, when exposed to a LD cycle, exhibited activity distributions over time (Figs. 41, 42, 43) which were almost identical to those shown after the swimming frenzy had subsided. The presence or absence of twilight in the photophase had no effect on this feature of activity. Swimming activity was bimodally distributed in the presence of twilight, and was concentrated in the photophase.

The same was true for Ascension Island hatchlings exposed to a LD cycle. When older, these latter showed a stronger daily activity pattern than the hatchlings from Costa Rica (Figs. 44, 45). They did not, however, exhibit infradian or ultradian cycles during their swimming frenzy. These developed immediately after cessation of the infantile frenzy.

Under constant light, approximately half of all the hatchlings tested showed a statistically significant circadian period of swimming activity during the swimming frenzy (Fig. 46) which was equivalent to that shown by older turtles of the same population. The remainder did not exhibit a circadian periodicity in their swimming activity (Fig. 47) until after cessation of the frenzy. Minor tidal effects were distinguishable in all the records, whether or not a periodic light cue was present.

As the hatchlings grew older, they tended to spend more of their active time diving and swimming near the bottom of the tanks. During the frenzy, almost no subsurface activity was recorded, but by the age of four months, the turtles spent more than half their active time under

Figure 41. Representative plots of the distribution of swimming activity over time on the first, sixth, and eleventh days in the water of two green turtle hatchlings from Tortuguero, Costa Rica. Data were plotted as deviations of three-hour moving means from the daily average activity index.
LD+t13:11(270:0.1)

1
6
11
30
0
-30
10
0
-10
20
0
-20
20
10
0
-10
20
10
0
-10
0800
2000
Deviation from Mean
Time of Day

ns of th
vity rec
a Rica,
13:11(27

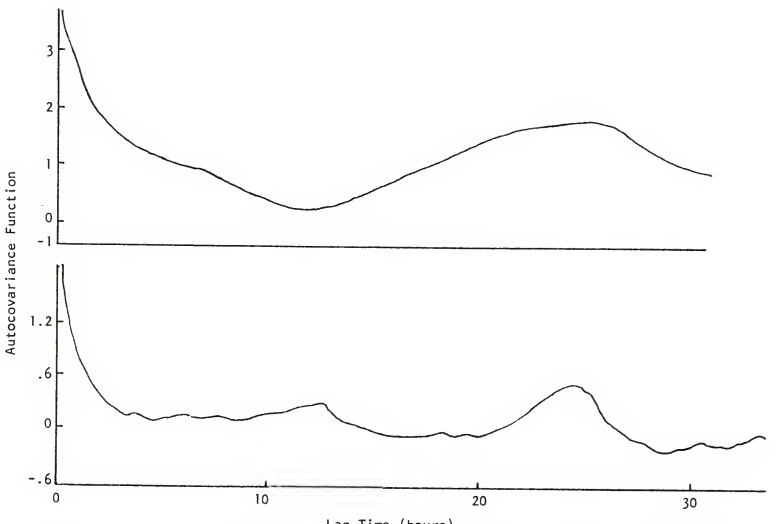
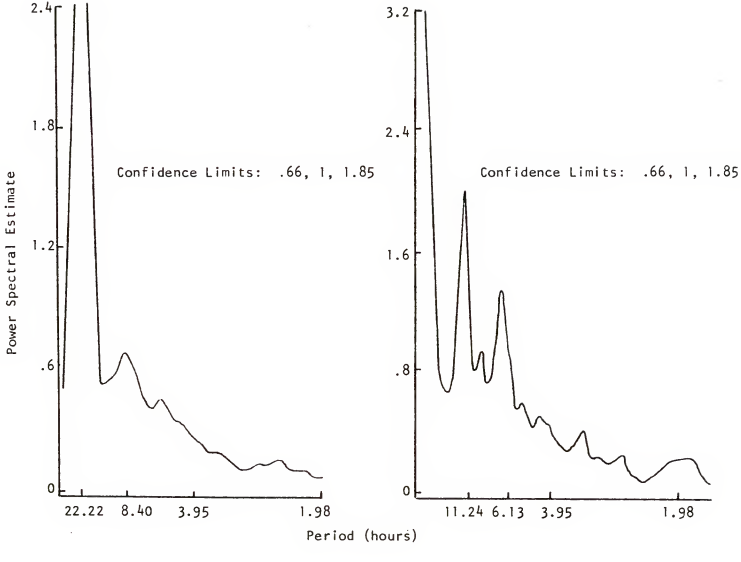


Figure 42. Graphs of the autocovariance functionsof the swimming frenzy activity records of two green turtle hatchlings from Tortuguero, Costa Rica, plotted against time. LD+t13:11(270:0.1)

Figure 43. Graphs of the power spectral estimates of the swimming frenzy activity records of two hatchling green turtles from Tortuguero, Costa Rica, plotted against period.
LD+t13:11(270:0.1)


2.4
1.8
1.2
.6
0
Power Spectral Estimate
Confidence Limits: .66, 1, 1.85
22.22 8.40 3.95 1.98
3.2
2.4
1.6
.8
0
Confidence Limits: .66, 1, 1.85
11.24 6.13 3.95 1.98
Period (hours)

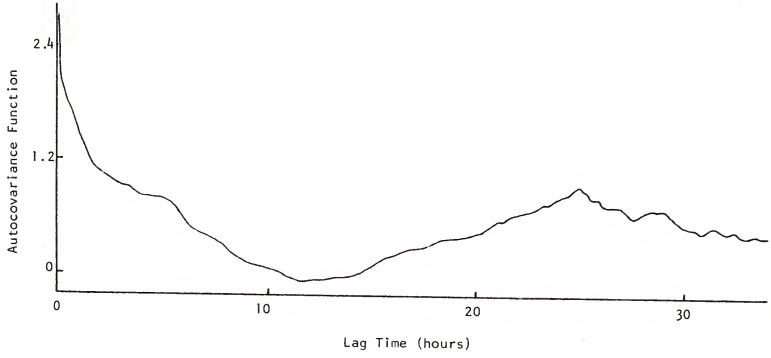


Figure 44. Graph of the autocovariance function of the swimming frenzy activity record of a green turtle hatchling from Ascension Island. LD+t12:12(270:0.1)

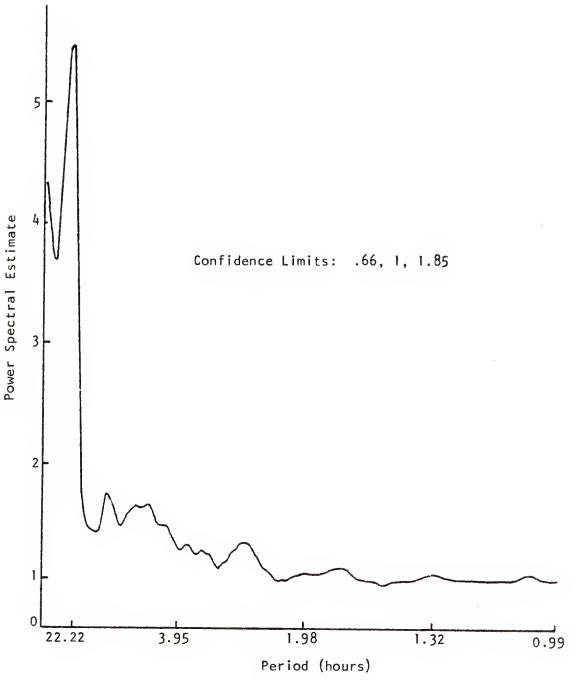
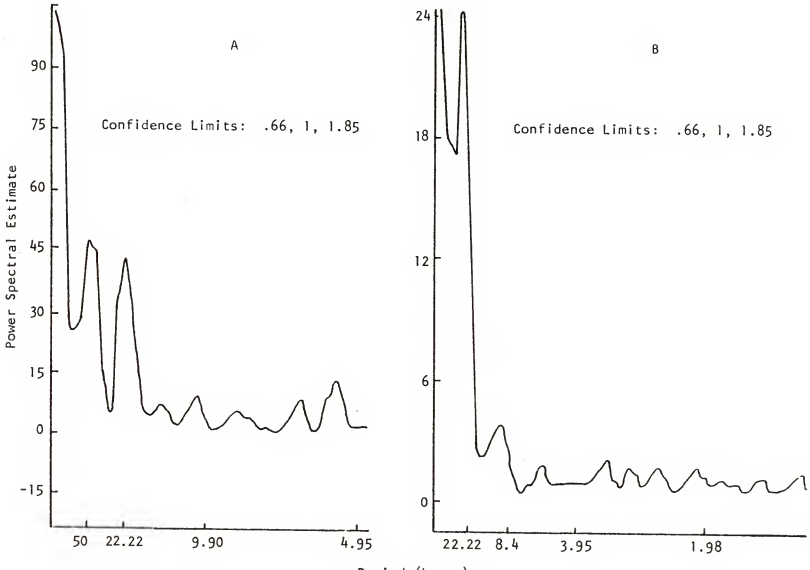


Figure 45. Graph of the power spectral estimates of the swimming frenzy activity record of a green turtle hatchling from Ascension Island, plotted against period. LD+t12:12(270:0.1)

Figure 46. Graphs of the power spectral estimates of the swimming frenzy activity records of two green turtle hatchlings, one from Tortuguero, Costa Rica (A) and one from Ascension Island (B), plotted against period.
LL(270)


A
Confidence Limits: .66, 1, 1.85
90
75
60
45
30
15
0
-15
50
22.22
9.90
4.95
B
Confidence Limits: .66, 1, 1.85
24
18
12
6
0
22.22
8.4
3.95
1.98
Power Spectral Estimate
Period (hours)

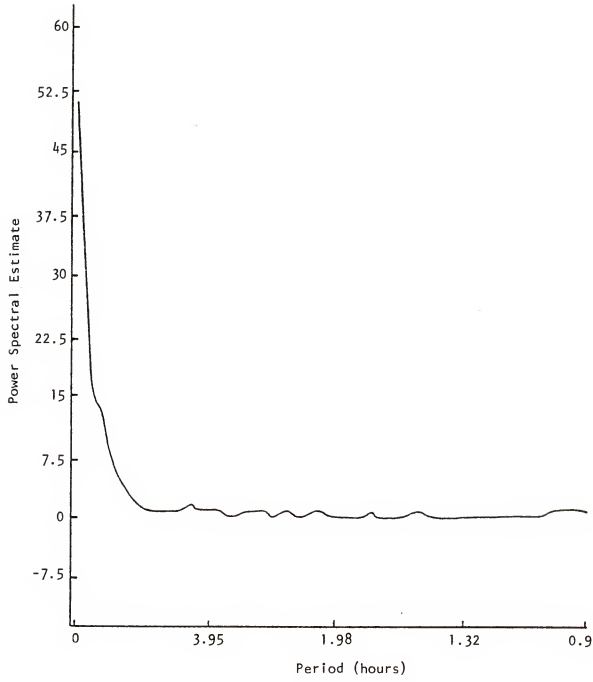


Figure 47. Graph of the power spectral estimates of the swimming frenzy activity record of a green turtle hatchling from Ascension Island, plotted against period.
LL(270)

the surface. This is probably related to the development of buoyancy control (Milsom 1975) which enables the turtle to swim at depth without undue expenditure of energy.

It seems, then, that the basic temporal pattern of swimming activity is shown by turtles from the time of their initial entry to water. The increased amounts of swimming activity during the frenzy, superimposed on the basic swimming pattern, may make the pattern somewhat difficult to distinguish visually, but do not actually extinguish the pattern.

APPENDIX I
THE ANALYSIS OF BIOLOGICAL TIME SERIES

The disposition toward periodic behavior is a characteristic of living systems and the focal point of biorhythm research. The analysis of biorhythm data is difficult (Klopfer and Hailman 1967) and the difficulties are compounded when one is concerned with both circadian and infradian or ultradian rhythms. Only recently have sophisticated statistical techniques been brought to bear upon the problem.

Mercer (1960), during the Cold Spring Harbor Symposium on Biological Clocks, pointed out that classical methods such as Fourier analysis are inadequate when apparently random components are present in a periodic series, the usual case for biological data. These random, or non-deterministic, time series are best analyzed by methods based on non-linear statistical mechanics (Enright 1965) such as autocovariance and spectral analysis (Mercer 1960). The following is a brief summary of techniques of time series analysis used in this paper. More exhaustive treatments of the subject are readily available (see for example Blackman and Tukey 1958, Bendat 1962, Jenkins and Watts 1968, Campbell and Shipp 1974).

A time series is any sequence of numbers which represents a progression of some parameter in time (Platt and Denman 1975). It is a function $x(t)$ of time t. The future behavior of the non-deterministic time series cannot be predicted exactly, but the average properties of the series can be calculated.

Consider a discrete time series composed of a finite number of N equally spaced data points:

$$x_t, \qquad t = 1,2,\ldots,N.$$

It is necessary for application of the techniques in question to assume that the series obeys a normal probability distribution and is stationary; that is, the mean and variance of the series do not change with time (Jenkins and Watts 1968). Ergodicity of the data must also be assumed. The time averages of a single record or series must be equivalent to the ensemble averages of a large collection of records (Bendat 1962). These assumptions are vital when the number of records is limited, and visual examination of the data I subjected to these analyses gave no reason to question these assumptions.

The autocovariance function can be estimated in practice as

$$C_{xx}(u) = N^{-1} \sum_{t=1}^{N-u} (x_t - \bar{x})(x_{t+u} - \bar{x}), \quad u = 0,1,2,\ldots,L \quad (1)$$

where $$\bar{x} = N^{-1} \sum_{t=1}^{N} x_t$$

which is the mean of the observed time series (Jenkins and Watts 1968). The plot of $C_{xx}(u)$ versus u is the sample autocovariance function of the time series. It has a maximum at $u = 0$ and is an even function of u. That is,

$$C_{xx}(u) = C_{xx}(-u)$$

so that only the time from 0 to L need to be considered.

The comparison of two time series requires calculation of the crosscovariance function according to

$$C_{xy}(u) = \begin{cases} N^{-1} \sum_{t=u+1}^{N} (x_t - \bar{x})(y_{t+u} - \bar{y}) \\ N^{-1} \sum_{t=1}^{N-u} (x_{t+u} - \bar{x})(y_t - \bar{y}), \quad u = 0,1,2,\ldots,L \end{cases} \quad (2)$$

where $\bar{x} = N^{-1} \sum_{t=1}^{N} x_t$ and $\bar{y} = N^{-1} \sum_{t=1}^{N} y_t$

are the means of the observed time series. The crosscovariance function, unlike the autocovariance function, does not have a maximum at u=0. The function is an uneven one, giving information on both frequency and phase angle, and lags must be made in both directions.

Plots of autocovariance and crosscovariance functions may be sufficient if they show strong evidence of periodicity. It is often desirable, however, to subject these functions to Fourier cosine and sine transformations respectively in order to obtain the spectral density function of the series. When plotted, each point in the resultant power spectrum represents a mean power over a specified frequency (or period) range (Mercer 1960). It is best to plot the logarithm of the spectrum, as this shows more detail in the spectrum over a wider amplitude range (Jenkins and Watts 1968). The non-logarithmic plots were considered adequate in this study, however, and so have been duplicated here, although both were computed for examination.

With the autocovariance values as input, the digital computing formula of the smoothed autospectral density function is

$$\bar{C}_{xx}(f) = 2\{c_{xx}(0) + 2 \sum_{u=1}^{L-1} (u)w(u)\cos 2\pi f u\} \quad 0 \leq f \leq 1/2 \qquad (3)$$

(Jenkins and Watts 1968). The upper frequency limit of 1/2, the Nyquist frequency, is related to the original interval between data readings so that the shortest periodicity which can be identified is double the sampling interval, since $\tau = 1/f$. Thus, the sampling interval must be small enough to allow estimation of the spectrum in the range of interest. In this study, I used sampling ranges of 10, 30 and 60 minutes and a period of 20 minutes was therefore the shortest which could be defined.

Smoothing of the autospectrum is facilitated by limiting the number of lags to L-1 and inserting an appropriate lag window, $w(u)$, in the computing formula. The Tukey window,

$$w(u) = 0.5\ (1 + \cos \frac{\pi k}{L}) \tag{4}$$

is in common use (Campbell and Shipp 1974) and will be considered here. The spectral window, $W(u)$, is determined by taking the Fourier transform of the lag window (4) and has a bandwidth of

$$b = \frac{1.33}{L}. \tag{5}$$

The truncation point, L, must be chosen so as to reduce bias in the estimate. If the width of the narrowest important peak in the future spectrum (a) can be guessed, then the truncation point may be determined by

$$L = \frac{1.33}{a\Delta}$$

(Campbell and Shipp 1974). That is, the discrete autocovariance function and power spectral density function must be computed to $\frac{1.33}{a\Delta}$ lags. The value of a for the turtles was estimated at 0.17 hours from examination of the original activity records. The relationship $b < a$ must be maintained (Jenkins and Watts 1968). For the BMD 02T program used (Dixon 1971), the number of data points was limited to 1000 and the number of computation lags to 199. A sampling interval of 10 minutes allowed the analysis of approximately seven days of data at one time.

The confidence limits about a spectral density estimate are

$$\frac{\nu \bar{C}_{xx}\ (f)}{\chi_{\nu}\{1-(\alpha/2)\}}\ ,\ \frac{\nu \bar{C}_{xx}\ (f)}{\chi_{\nu}(\alpha/2)}$$

where α is the probability of a theoretical spectrum falling beyond its confidence limits (Campbell and Shipp 1974). For an 80% confidence

interval, α = 1.0 - 0.8 or 0.2. The number of degrees of freedom, ν, using the Tukey window, is 2.667 (N/L), where N is the number of data points worked with.

APPENDIX II
SYMBOLS AND ABBREVIATIONS

An attempt has been made in this paper to use symbols and abbreviations in accordance with biological rhythm and time series analysis literature. Those referring to circadian rhythms (Table 8) are used as recommended by Aschoff *et al.* (1965). Jenkins and Watts (1968) provide the source of most of the time series symbols (Table 9) and formulae. In some cases, a particular symbol may have a different meaning when taken in the context of different fields of study and care must be taken to note the context in which they are used here.

Table 8. A summary of biological rhythm symbols and abbreviations used in the text of this paper.

ψ	Phase angle of biological oscillation
$\Delta\psi$	Amount of shift of phase angle
Φ	Phase angle of Zeitgeber
$\Delta\Phi$	Amount of shift of phase angle
Ψ	Φ-ψ; phase angle difference between Zeitgeber and biological oscillation
LD	Light-dark cycle (LL = continuous light, DD = continuous dark)
LD+t	Light-dark cycle with twilight (dawn and/or dusk) during the L
L	Light time (photophase)
D	Dark time (scotophase)
$LDx_1:x_2$	LD cycle with x_1 hours of light followed by x_2 hours of dark
$LDx_1:x_2(y_1:y_2)$	LD cycle with light intensity y_1 during x_1 and y_2 during x_2 (intensity given in lux)
α	Active time
ρ	Rest time
l	Cumulative activity index (AI) in L
d	Cumulative AI in D
s	Cumulative AI in α hours
r	Cumulative AI in ρ hours

Table 9. A summary of the time series analysis symbols and abbreviations used in the text of this paper.

T	Record length (hours)
f	Frequency
τ	1/f, period of the rhythm
t	time that an event x (or y) occurred
Δ	time or sampling interval
N	Number of t values observed
ν	Degrees of freedom
L	Truncation point; the number of lags to which the autocovariance function (acvf), the crosscovariance (ccvf) or the power spectrum (ps) is computed
a	Narrowest width of peak which may be identified in the spectrum
b	Bandwidth of the lag window
α	Probability of a theoretical spectrum falling beyond its confidence limits
$c_{xx}(u)$	Autocovariance function estimate
$c_{xy}(u)$	Crosscovariance function estimate
$\bar{C}_{xx}(f)$	Smoothed power spectral density estimate
u	Displacement or lag = 0,1,2,...,L
$w(u)$	Lag window
$W(u)$	Spectral window

LITERATURE CITED

Ackerman, R. A. 1975. Diffusion and the gas exchange of sea turtle eggs. Ph.D. Dissertation. University of Florida.

Anonymous. 1955. Atlas of pilot charts. Central American waters and South Atlantic Ocean. U.S. Navy Hydrographic Office, Washington, D.C. Pub. No. 108.

Anonymous. 1967. Atlas of the North Atlantic Ocean. Section II: Physical properties. U.S. Navy Oceanographic Office, Washington, D.C. Pub. No. 700.

Aschoff, J. 1960. Exogenous and endogenous components in circadian rhythms. Cold Spring Harbor Symp. Quant. Biol. 25: 11-28.

Aschoff, J. 1963. Comparative physiology: Diurnal rhythms. Ann. Rev. Physiol. 25: 581-600.

Aschoff, J. 1965. The phase angle difference in circadian periodicity. IN *Circadian Clocks*. J. Aschoff, ed. North Holland, Amsterdam. pp. 262-276.

Aschoff, J. 1966. Circadian activity patterns with two peaks. Ecology 47: 657-662.

Aschoff, J. 1969. Phasenlage der Tagesperiodik in Abhängigkeit von Jahreszeit und Breitengrad. Oecologia (Berl.) 3: 125-165.

Aschoff, J., K. Klotter, and R. Wever. 1965. Circadian vocabulary. IN *Circadian Clocks*. J. Aschoff, ed. North Holland, Amsterdam. pp. x-xviii.

Beck, S. D. 1968. *Insect Photoperiodism*. Academic Press, N.Y.

Bendat, J. S. 1962. Interpretation and application of statistical analysis for random physical phenomena. IRE Trans. Biomed. Elect. 9: 31-43.

Blackman, R. B. and J. W. Tukey. 1958. The measurement of power spectra from the point of view of communications engineering. Bell Syst. Tech. J. 37: 185-282.

Blackman, R. B. and J. W. Tukey. 1958. The measurement of power spectra from the point of view of communications engineering. Bell Syst. Tech. J. 37: 485-569.

Brett, W. J. 1971. Persistent rhythm of locomotion activity in the turtle *Pseudemys scripta*. Comp. Biochem. Physiol. 40A: 925-934.

Brown, F. A., Jr. and E. D. Terracini. 1959. Exogenous timing of rat spontaneous activity patterns. Proc. Soc. Exper. Biol. Med. 101: 457-460.

Bünning, E. 1973. *The Physiological Clock*. 3rd ed. Springer-Verlag, N.Y.

Bustard, H. R. 1967. Mechanism of nocturnal emergence from the nest in green turtle hatchlings. Nature 214: 317.

Campbell, D. J. and E. Shipp. 1974. Spectral analysis of cyclic behavior with examples from the field cricket *Teleogryllus commodus* (Walk.). Anim. Behav. 22: 862-875.

Carr, A. F. 1962. Orientation problems in the high seas travel and terrestrial movements of marine turtles. Amer. Sci. 50: 359-374.

Carr, A. F. 1965. The navigation of the green turtle. Sci. Am. 212: 141-149.

Carr, A. F. 1972. The case for long-range chemoreceptive piloting in *Chelonia*. NASA Sp-262: 469-483.

Carr, A. F. 1975. The Ascension Island green turtle colony. Copeia 1975: 547-555.

Carr, A. F., M. H. Carr and A. B. Meylan. 1978. The ecology and migration of sea turtles, 7. The West Caribbean green turtle colony. Bull. Amer. Mus. Nat. Hist. 162: 1-46.

Carr, A. F. and P. J. Coleman. 1974. Sea floor spreading theory and the odyssey of the green turtle. Nature 249: 128-130.

Carr, A. F. and L. Ogren. 1960. The ecology and migrations of sea turtles, 4. The green turtle in the Caribbean Sea. Bull. Amer. Mus. Nat. Hist. 121: 1-48.

Dann, S. 1976. Light intensity and timing of daily activity in finches. Ibis 118: 223-236.

Dann, S. and J. Aschoff. 1975. Circadian rhythms of locomotor activity in captive birds and mammals: Their variation with season and latitude. Oecologia (Berl.) 18: 269-316.

DeCoursey, P. J. 1961. Effect of light on the circadian activity rhythm of the flying squirrel, *Glaucomys volans*. Z. vergl. Physiol. 44: 331-354.

Dixon, W. J. (ed.) 1971. *BMD Biomedical Computer Programs*. Univ. Calif. Publications in Automatic Computation. Number 2. Univ. Calif. Press, L.A.

Elenbaas, W. (ed.). 1971. *Fluorescent Lamps*. 2nd ed. MacMillan, London.

Enright, J. T. 1965. The search for rhythmicity in biological time-series. J. Theoret. Biol. 8: 426-468.

Enright, J. T. 1970. Ecological aspects of endogenous rhythmicity. Ann. Rev. Ecol. Syst. 1: 221-238.

Eskin, A. 1971. Some properties of the system controlling the circadian activity rhythms of sparrows. IN *Biochronometry*. M. Menaker, ed. Proc. Natl. Acad. Sci., Washington, D.C. pp. 55-80.

Fingerman, M. 1960. Tidal rhythmicity in marine organisms. Cold Spring Harbor Symp. Quant. Biol. 25: 481-489.

Fischer, K. 1964. Spontanes Richtungsfinden nach dem Sonnenstand bei *Chelonia mydas* L. (Suppenschildkröte). Die Naturwissenschaften 51: 203.

Fletemeyer, J. R. 1978. Underwater tracking evidence of neonate loggerhead sea turtles seeking shelter in drifting Sargassum. Copeia 1978: 148-149.

Frick, J. 1976. Orientation and behavior of hatchling green turtles (*Chelonia mydas*) in the sea. Anim. Behav. 24: 849-857.

Gwinner, E. 1974. Testosterone induces "splitting" of circadian locomotor activity rhythms in birds. Science 185: 72-74.

Halberg, F. 1959. Physiologic 24-hour periodicity; general and procedural conditions with reference to the adrenal cycle. Z. f. Vitamin-, Hormon- and Ferment- forschung. 10: 225-296.

Harker, J. E. 1960. The effect of perturbations in the environmental cycle on the diurnal rhythm of *Periplaneta americana* L. J. exp. Biol. 37: 154-163.

Hirth, H. and W. M. Schaffer. 1974. Survival rate of the green turtle, *Chelonia mydas*, necessary to maintain stable populations. Copeia 1974: 544-546.

Hoffmann, K. 1968. Synchronisation der circadianen Aktivitätsperiodik von Eidechsen durch Temperaturcyclen verschiedener Amplitude. Z. vergl. Physiol. 58: 225-228.

Hoffmann, K. 1971. Splitting of the circadian rhythm as a function of light intensity. IN *Biochronometry*. M. Menaker, ed. Proc. Natl. Acad. Sci. Washington, D.C. pp. 134-150.

Jenkins, G. M. and D. G. Watts. 1968. *Spectral Analysis and its Applications*. Holden Day, San Francisco.

Kaufmann, R. 1972. Wachstumsraten in Gefangenschaft gehaltener Meeresschildkröten. II. Mitt. Inst. Colombo-Alemán Invest. Cient 6: 105-112.

Kenagy, G. J. 1976. The periodicity of daily activity and its seasonal changes in free-ranging and captive kangaroo rats. Oecologia (Berl.) 24: 105-140.

Klopfer, P. H. and J. P. Hailman. 1967. *An Introduction to Animal Behavior: Ethology's First Century*. Prentice-Hall, Toronto.

Kooistra, T. A. and D. H. Evans. 1976. Sodium balance in the green turtle, *Chelonia mydas*, in seawater and freshwater. J. Comp. Physiol. 107: 229-240.

Menaker, M. 1976. Overview. A "terrestrial" biologist looks at biorhythms in the marine environment. IN *Biological Rhythms in the Marine Environment*. P. J. DeCoursey, ed. Univ. of S. Carolina Press, Charleston. pp. 273-279.

Mercer, D. M. A. 1960. The behavior of multiple oscillator systems. IN *Circadian Clocks*. J. Aschoff, ed. North Holland, Amsterdam. pp. 64-73.

Meylan, A. B. 1978. The behavioral ecology of the west Caribbean green turtle (*Chelonia mydas*) in the internesting habitat. M.S. Thesis, University of Florida.

Milsom, W. K. 1975. Development of buoyancy control in juvenile Atlantic loggerhead turtles, *Caretta c. caretta*. Copeia 1975: 758-762.

Mrosovsky, N. 1968. Thermal emergence of hatchling sea turtles: Control by thermal inhibition of activity. Nature 220: 1338-1339.

Mrosovsky, N. 1977. Individual differences in the sea-finding mechanism of hatchling leatherback turtles. Brain, Behav. Evol. 14: 261-273.

Mrosovsky, N. 1978. Effects of flashing lights on sea-finding behavior of green turtles. Behav. Biol. 22: 85-91.

Mrosovsky, N. and A. F. Carr. 1967. Preference for light of short wavelengths in hatchling green sea turtles, *Chelonia mydas*, tested on their natural nesting beaches. Behaviour 28: 217-231.

Mrosovsky, N. and S. J. Shettleworth. 1968. Wavelength preferences and brightness cues in the water finding behavior of sea turtles. Behaviour 32: 211-257.

Mrosovsky, N. and S. J. Shettleworth. 1974. Further studies on the sea-finding mechanism in green turtle hatchlings. Behaviour 51: 195-208.

Palmer, J. D. (ed.) 1970. *The Biological Clock: Two Views*. Academic Press, N.Y.

Philibosian, R. 1976. Disorientation of hawksbill turtle hatchlings, *Eretmochelys imbricata*, by stadium lights. Copeia 1976: 824.

Pittendrigh, C. S. 1960. Circadian rhythms and the circadian organization of living systems. Cold Spring Harbor Symp. Quant. Biol. 25: 159-184.

Pittendrigh, C. S. 1974. Circadian oscillations in cells and the circadian organization of multicellular systems. IN *The Neurosciences. Third Study Program*. F. A. Schmitt, ed. MIT Press, Cambridge. pp. 437-458.

Pittendrigh, C. S. and S. Dann. 1976. A functional analysis of circadian pacemakers in nocturnal rodents. IV. Entrainment: Pacemaker as clock. J. Comp. Physiol. 106: 291-331.

Platt, T. and K. L. Denman. 1975. Spectral analysis in ecology. Ann. Rev. Ecol. Syst. 6: 189-210.

Pritchard, P. C. H. 1976. Post-nesting movement of marine turtles (Cheloniidae and Dermochelyidae) tagged in the Guianas. Copeia 1976: 749-754.

Raj, U. 1976. Incubation and hatching success in artificially incubated eggs of the hawksbill turtle, *Eretmochelys imbricata* (L.). J. exp. mar. Biol. Ecol. 22: 91-99.

Richardson, N. E. and J. McCleave. 1974. Locomotor activity rhythms of juvenile Atlantic salmon (*Salmo salar*) in various light conditions. Biol. Bull. 147: 422-432.

Schwassmann, H. O. 1971a. Biological rhythms. IN *Fish Physiology* (Vol. 6). W. S. Hour and D. J. Randall (eds.) Academic Press, N.Y. pp. 371-428.

Schwassmann, H. O. 1971b. Circadian activity pattern in Gymnotid electric fish. IN *Biochronometry*. M. Menaker (ed.). Proc. Natl. Acad. Sci., Washington, D.C. pp. 186-199.

Snedecor, G. W. and W. G. Cochrane. 1967. *Statistical Methods*. 6th ed. Iowa State Univ. Press. Ames, Iowa.

Sokal, R. R. and F. J. Rohlf. 1969. *Biometry, the Principles and Practice of Statistics in Biological Research*. W. H. Freeman and Co., San Francisco.

Weast, R. C. (ed.) 1972. *Handbook of Chemistry and Physics*. 53 ed. Chemical Rubber Co., Cleveland, Ohio.

Webb, H. M. and F. A. Brown, Jr. 1959. Interaction of diurnal and tidal rhythms in the fiddler crab, *Uca pugnax*. Biol. Bull. 129: 582-591.

Weyl, P. K. 1978. Micropaleontology and ocean surface climate. Science 202: 475-481.

Witham, P. 1976. Evidence for ocean-current mediated dispersal in young green turtles, *Chelonia mydas* (Linnaeus). M.S. Thesis, University of Oklahoma.

Witham, R. and C. R. Futch. 1977. Early growth and oceanic survival of pen-reared sea turtles. Herpetologica 33: 404-409.

Zwinenberg, A. J. 1976. The olive ridley, *Lepidochelys olivacea* (Eschcholtz, 1829): Probably the most numerous marine turtle today. Bull. Maryland Herp. Soc. 12: 75-95.

BIOGRAPHICAL SKETCH

Sheri A. Dalton was born in 1946 in Saskatchewan, Canada. She graduated from high school in Clarkson, Ontario, and later attended the University of Western Ontario, London, where she received a Bachelor of Science degree in Zoology. A Master of Arts degree in Biology was awarded her by Mount Holyoke College, Massachusetts, and she then entered the Department of Zoology of the University of Florida where she completed the requirements for the Doctor of Philosophy in zoology.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

J. H. Kaufmann, Chairman
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Archie Carr
Graduate Research Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

H. O. Schwassmann
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

M. C. Yang
Associate Professor of Statistics

This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

June, 1979

_____

Dean, Graduate School